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# THE JOURNAL

OF

# Comparative Neurology

A QUARTERLY PERIODICAL DEVOTED TO THE  
Comparative Study of the Nervous System.

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THE FINER STRUCTURE OF THE SELACHIAN CEREBELLUM (MUSTELUS VULGARIS) AS SHOWN BY CHROME-SILVER PREPARATIONS.

By DR. ALFRED SCHAPER,  
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(WITH PLATES I TO IV AND ONE FIGURE IN THE TEXT.)

During my stay at the Marine Biological Laboratory at Woods Hole, Mass., in the summer of 1897, I found opportunity to extend my comparative anatomical studies on the cerebellum over the various species of Selachii to be found on that coast. I especially endeavored, among other things, to elucidate by means of the *Golgi method* the finer structure of the cerebellum of this group of vertebrates, so important from a comparative anatomical standpoint. Notwithstanding the zeal with which the various representatives of the vertebrate phylum have been investigated by means of the Golgi method during the last decade, the selachian brain has hitherto, strange to say, scarcely been included within the range of research. The first and only author so far who has given us a connected description of the histological structure of the selachian brain is, as far as I know, *E. Sauerbeck* (4). The specimens at this author's disposal were prepared by Professor Rudolf Burckhardt of Basel, under whose direction the work was prosecuted. Sauerbeck's results appeared in an article in Band XII of the *Anatomischer Anzeiger* under the title "*Beiträge zur Kenntniss vom feineren Bau des Selachierhirns.*" Although this work, as the author himself states, makes no claim to completeness, yet it is the first attempt to fill in this existing gap in our comparative histological knowledge of the central nervous system and thereby can serve as a worthy starting-point for further and more thorough studies in this field.

In all researches on the central nervous system by means of impregnations the elements of the cerebellum, as is well known, offer the greatest difficulties. A considerable number of preparations are usually required to demonstrate all the elements of this organ. This peculiarity appears to have presented itself also in the preparations at Sauerbeck's service, as, judging from his figures, all the other parts of the brain seem to have been much more completely and certainly impregnated than the cerebellum. Thus Sauerbeck was able to demonstrate only *Purkinje cells* and *ependyma elements* in the cerebellum. He has, indeed, on the ground of stained preparations confirmed the presence of a molecular and a granular layer in agreement with earlier authors (Viault (8), Sanders (3), and Rohon (2)), yet he did not succeed with Golgi preparations in learning anything of the elements constituting them. Thus there remain in reserve many important points for further investigation to determine. As I have several years since directed my special attention to the morphology of the cerebellum and contemplate subjecting this part of the brain in all the vertebrate types to a comparative anatomical and comparative embryological investigation, the present gap in our knowledge of the selachian brain, so important for my purpose, became so much the more perceptible to me. It was natural, therefore, that I should eagerly seize the opportunity, presenting itself to me in Woods Hole, of filling in, as far as lay in my power, these gaps by means of suitable investigations. My efforts toward this end were attended with some success and I take the liberty to report briefly upon them in the following.

Although I propose to publish here the results obtained from silver preparations only, yet I might for general orientation, preface this with a few words upon the morphology of the selachian brain. In so doing I confine myself to that of *Mustelus vulgaris* (*Galeus canis*) from which species my Golgi preparations were exclusively made.

As with most of the Selachii, in *Mustelus* the cerebellum is greatly developed and is traversed by numerous transverse folds. It might from this appear that the cerebellum of the



shark already approaches that of the higher vertebrates in its morphological structure. This, however, is not the case. On a closer examination we soon learn *that we have to do only with a plate thrown into transverse folds and enclosing a relatively roomy cavity, not with a solid organ like that of birds and mammals.* The essential feature in the cerebellum of the latter is the massive development of the white matter, which goes hand in hand with an extraordinarily complicated surface folding of the cortex, whence the formation of the "*arbor vitae*" so characteristic of birds and mammals. *There is none of this present in the selachian cerebellum.* There is expressed, indeed, in the folding an evident tendency to an extension of the surface, yet these folds cannot be directly (also not genetically) homologized with the "convolutions" and furrows of the cerebellum of the higher vertebrates. In the first case we have, in general, at least, to do with *actual folds*, i. e. with structures where an infolding on one side of the lamella corresponds to an outfolding on the other, while in the second case we are concerned with *solid* ridges and protuberances separated by furrows.

Concerning the finer structure, the presence of the three cerebellar layers typical for all vertebrates—the molecular, Purkinje and granular—has been already demonstrated by the earlier authors, as Viault (8), Sanders (3) and Rohon (2). I have to add, however, that the granular layer does not everywhere participate to the same extent in the structure of the cerebellar lamella. Indeed in definite and extensive portions of the latter it is entirely *absent*, in consequence of which the cortical matter in these places consists of the molecular and Purkinje layers only and the latter is separated from the ependymal layer by only a relatively thin zone of fibers. The Purkinje cells likewise are absent in certain regions of the lamella. This relation of the layers is in various respects of especial interest but I cannot enter into this here. The accompanying schema of a transverse section through the anterior portion of the cerebellum of *Mustelus* may serve to illustrate this condition.

I might however add that in the Selachii *during life*, as in younger stages in bony fishes and in certain embryonic periods of all vertebrates the *cerebellar lamella* has a *deep longitudinal furrow in the median line* (*sulcus medianus*) where the extremely thin lamella is composed solely of ependyma cells and commissural fibers.

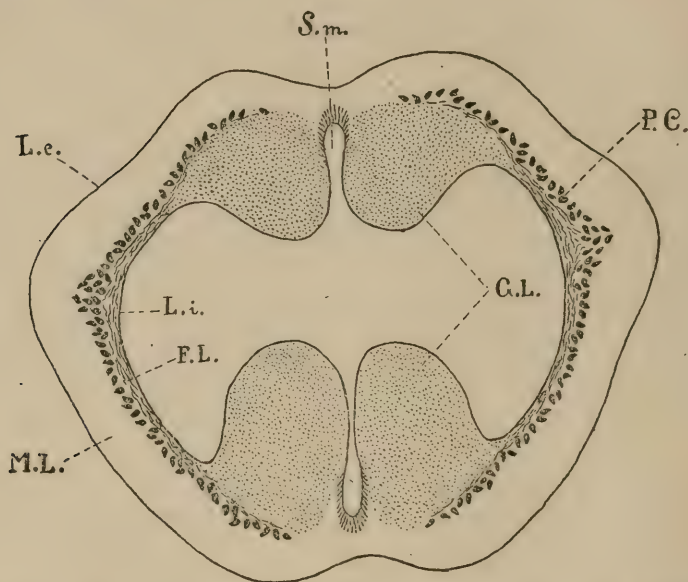


Diagram: Cross-section through the anterior part of the cerebellum of *Mustelus vulgaris* showing the arrangement of the different layers.

I pass now to a description of my silver preparations and begin with the most characteristic cell group of the cerebellum, the

#### *Purkinje Cells.*

The presence of these cells has been already established by the older investigators (Viault, Sanders and Rohon). Sauerbeck was the first, though, to observe and describe them in *Golgi preparations*. He speaks of them as follows: "Von der Membrana limitans interna ab gerechnet im zweiten Drittel der radialen Ausdehnung (der Kleinhirnlamelle) finden sich typische Purkinje-Zellen, die nach innen, d. h. gegen die nicht versilberte



Körnerschicht hin, einen Axencylinder senden, der sehr bald in die horizontale, resp. tangentielle Richtung umbiegt; nach aussen ragen armleuchterartige Dentrifenfortsätze, doch sind diese nicht so reich verzweigt wie bei höheren Vertebraten, wie auch schon bei den Teleostiern *Schaper* sie abgebildet hat." The figures given by Sauerbeck are, in consequence of their small scale, but little adapted to reproduce the characteristics of these cells. I have therefore again represented two typical forms of Purkinje cells in Plate I, Figs. 1 and 2. We see from these that the size and form of the cell-body, as well as the magnitude and arrangement of the protoplasmic processes, are subject to considerable variation. This is correlated in part with the very variable thickness of the molecular layer; we meet the more massive and coarser type (Plate I, fig. 1) mostly in the more strongly developed portions of the molecular layer, the smaller and more delicate type (Plate I, fig. 2) mostly in the thinner regions of this layer. As Sauerbeck rightly remarks, the protoplasmic processes are not so richly branched as is usually the case among the higher vertebrates and one can compare them in this respect with those of the bony fishes, as some time ago (5) described and figured by me. They are distinguished, however, even from the latter by a still more sparse arborization and their less straight, irregular course to the surface. One could say *they stand upon a still lower plane of development than those of the bony fishes and display throughout life an embryonic condition of the homologous cells of the higher vertebrates.* Like the dendrites of all Purkinje cells, these are provided with a thick covering of very fine spines and usually tend to terminate with a slight thickening.

Concerning the *axis-cylinder*, this also presents certain noteworthy peculiarities. With respect to their course, they behave differently according as they come from cells which have a granular layer beneath them or from such as, in the absence of the granular layer, lie close to the *membrana limitans interna*. (See text-figure, p. 4). In the latter case (Plate I, fig. 1) the axis-cylinder is naturally compelled, soon after its origin from the under pole of the cell, to bend laterally and proceed,

parallel with the *limitans interna* and immediately beneath the row of Purkinje cells, to its destination. In the preparation upon which figure 1 is based I succeeded in following such an axis-cylinder a considerable distance. In this way the neuraxons of those Purkinje cells situated in the cerebellar plate where a granular layer is lacking furnish the principal contingent of the often considerable mass of parallel fibers interposed between the layer of Purkinje cells and the *limitans interna*. But even where there is a granular layer, the axis-cylinder does not as a rule immediately sink into this; but first proceeds a short distance in a horizontal direction and then takes a sharp bend inward (fig. 2). It is now to be noted that I never succeeded in any of my preparations in demonstrating *collaterals* of the axis-cylinders of the Purkinje cells, although, as far as I know, their presence has been established in all other vertebrates hitherto investigated. Whether we have here a defective impregnation or whether these collaterals are actually absent in the Selachii, and their absence is perhaps the expression of a lower phylogenetic stage of development, I do not venture to decide at present. Sauerbeck likewise does not mention collaterals in his article. Among his figures of Purkinje cells, however, are some with divided axis-cylinders. May one of these branches represent a collateral?

#### *Nerve-cells of the Molecular Layer.*

These cells are for the most part uncommonly delicate and vary extraordinarily in the form and size of the cell-body as well as in the mode of branching of their protoplasmic processes. To properly illustrate this variety of form I have represented a larger number of cells in Plate I, figures 3 to 8. They lie in all levels of the molecular layer, from the layer of Purkinje cells (even pressing in between these) to close to the surface. The rule seems to obtain that the smaller the cells and the shorter their dendrites, the closer they lie to the surface and *vice versa*. The *dendrites* display in general the tendency to extend towards the surface, although in the deeper lying cells there is also a considerable extension of the same horizontally (Plate I, Fig. 3).



While the cells vary in form, yet the *neuraxons* in all the cells observed by me have essentially the same behavior. The nervous process soon loses its individuality through the giving off of very numerous lateral branches and is resolved a short distance from the cell body into its terminal arborization. Thus all the cells of the molecular layer belong to the so-called "*Golgi type*." In *course and mode of distribution*, however, the ramifications of these axis-cylinders display a certain variability; we find axis-cylinders which proceed horizontally a short distance and thereby give off lateral branches outward and inward (Plate I, figs. 3 and 7), others which descend and soon are lost in their terminal arborizations (Plate I, figs. 6 and 8) and others again which run outward in wide curves and then fall into more or less numerous terminal branches which mostly extend toward the surface (Plate I, figs. 4 and 5).

The question now arises: *What relation do these nervous processes bear to the Purkinje cells?* We know definitely that in the higher vertebrates, at least, a certain number of the cells of the molecular layer, the so-called "basket cells" enter into very close relation with the bodies of the Purkinje cells, embracing the latter with tassel-like terminal arborizations. Besides these, another group of cells of the molecular layer has long been known under the name of the "*star shaped*" or "*small cortical cells*" about whose axis-cylinder little was actually known. Stöhr (7) first succeeded about a year ago in demonstrating in silver-preparations of the human cerebellum well developed nervous processes on the "small cortical cells" also, whose terminal arborizations behave toward the Purkinje cells very much as the basket cells do, but without forming the typical basket of fibers. Stöhr is thereby inclined to *abandon the division of the cells of the molecular layer into basket cells and small cortical cells and to unite them all in one group with the common character that all, notwithstanding great differences of form, display the tendency to enter into close contact with the bodies of Purkinje cells by means of the ramifications of their axis-cylinders*. In this view Stöhr finds himself in agreement with Dogiel (1) and Kölliker who shortly before had similarly expressed

himself. Yet not long ago an article of Smirnow's (6) appeared, also an investigation of these elements of the cerebellum of man, as well as of the dog and hare. The results brought the author to the conclusion, in opposition to Stöhr's view, *that two distinct kinds of cells are to be distinguished in the molecular layer according to the behavior of the axis-cylinder.* The figures given in this work appear to me also to plainly show that there are cells in the molecular layer whose axis-cylinders do not bear comparison with those of the cells hitherto described as "*basket cells.*" In a number of these cells (in man also) the nervous process a short distance from its origin breaks up into numerous terminal arborizations which may be distributed in all directions. The field of distribution of many of these axis-cylinders does not extend down to the bodies of the Purkinje cells and if certain isolated branches do come into the neighborhood of the latter, yet, in view of the distribution in many directions of the remaining branches, this is to be regarded as an incidental appearance. The tassel-like arborization of the collaterals so characteristic of the basket cells can nowhere be demonstrated, at all events, with these cells. There appears, after all, to be only one characteristic applicable to all the cells of the molecular layer, viz.: *that their axis-cylinders soon break up into their terminal arborizations and generally do not leave the region of the molecular layer.* The *special* behavior of the axis-cylinders of the *individual* cells, however, that is the definite relations of *some* to the bodies of the Purkinje cells and the correlated typical adaptation of the terminal arborizations to the latter and the entirely disorderly mode of distribution of *other* cells, compels, or at least entitles us, in agreement with the conclusion of Smirnow previously given, *to distinguish two kinds of cells in the molecular layer, i. e. "basket cells" and the others accurately described by Smirnow which we still for the present may term "small cortical cells."* It is not thereby rendered necessary to create a *fundamental* distinction between these two categories of cells. It even appears probable to me that the basket cells are merely to be regarded *as a specialized form of the molecular cells.* Nevertheless the morphological differences in the behavior of the axis-cylinder



expressed in the higher vertebrates make the above division desirable from practical grounds.

I have entered into a discussion of this point more at length here to secure a basis for the elucidation of the relations which we have encountered in the above described cells of the molecular layer of the selachian cerebellum. As we have seen, the axis-cylinders of none of these cells exhibit the typical conduct of those of the basket cells; never were tassel-like terminal arborizations demonstrable. In certain cells lying in the deeper zone of the molecular layer, one sees here and there isolated terminal branches penetrate between the bodies of the Purkinje cells but there cannot be said to be the intimate and extensive contact-relation to the latter that there is in the case of the basket cells. Besides this, there are usually present on such axis-cylinders numerous other terminal branches which do not proceed towards the Purkinje cells. In the majority of the cells of the molecular layer we saw the ramifications of the axis-cylinder spread out in all directions without ever entering into any relation with the bodies of the Purkinje cells. *Thus all cells observed by me in the molecular layer of the selachian cerebellum more or less resemble—apart from a slighter complexity in the ramification of both dendrites and axis-cylinder—those cells which Smirnow has recently described in man and the higher vertebrates and distinguished from the true basket cells.* If we now, as mentioned above, will regard the basket cells merely as a particular specialization of the cells of the molecular layer, this specialization has not yet appeared in the cerebellum of the Selachii; *these cells are here still in a more primitive or phylogenetically younger stage of development.* I might use this opportunity to mention that I likewise have not hitherto succeeded in demonstrating true basket cells in the molecular layer of the cerebellum of *Telcosts* (5). Probably the state of affairs here is similar to that in the Selachii.

#### *Nerve-cells of the Granular Layer.*

The granular layer in the cerebellum of Selachii has hitherto been established as such and homologized with the cor-

responding layer of the higher vertebrates from stained preparations only. For such a homologization the proof was yet to be brought that this layer also contained similar *elements* and that these elements exhibited the same behavior as in the higher vertebrates.

I have now succeeded in my preparations in furnishing this proof, viz.: that there are both "small granule cells" (*granule cells sensu strictiori*) and "large granule cells" (so-called Golgi cells of the cerebellum) in the granular layer of the *Selachii*.

Regarding the *small granule cells* (Plate II, figs. 9, 10 and 11) the cell body and protoplasmic processes behave throughout like those of the higher vertebrates. The relatively small, mostly round or polygonal body sends in all directions a limited number (usually 3 or 4) of delicate protoplasmic processes of which the majority terminate in the way familiar in the other vertebrates, by means of a claw or brush-like structure.

The extremely thin *neuraxon* arises in the majority of cases from a protoplasmic process and then winds zig-zag between the other granules, usually proceeding directly to the molecular layer. When it reaches the molecular layer, *the axis-cylinder divides in a T in the manner typical for all vertebrates*. The two branches proceed in opposite directions parallel to the surface of the cerebellum and the long axis of its folds and finally (very probably a considerable distance from the point of bifurcation) break up into their terminal arborizations (Plate II, fig. 12). I have unfortunately only once succeeded (notwithstanding a most careful examination of my sections), in following one individual axis-cylinder of a granule cell without interruption from its origin to its point of division in the molecular layer. But I have repeatedly come upon the pieces of these T-shaped bifurcations, as shown in figure 12 (Plate II). There can scarcely be any doubt as to the connection of these fragments with the axis-cylinders of the granule cells and I have no hesitation in declaring, in spite of any inadequacy of observation, *that the behavior of the axis-cylinder of the small granule cells in the cerebellum of the Selachii is identical throughout with that in the other vertebrates*. I might mention here a certain peculiarity found



in the axis-cylinder of a granule cell, which I have figured in figure 9 (Plate II). We see here *the nervous process divide fork-like while still in the granular layer*. I recollect having once before happened upon a similar condition in the cerebellum of a mammal. We have here, doubtless, a *developmental anomaly* viz.: an abnormal division of the axis-cylinder.

I have above called attention to the fact that most of the nerve processes of the small granule cells appear to run in a more or less *direct* course to the molecular layer; frequently, however, one meets with cells also where the axis-cylinder first proceeds *horizontally* for a considerable stretch and then wends upward in a wide curve (Plate II, fig. 11 below). I have unfortunately not been able to follow such an axis-cylinder into the molecular layer. I conjecture however that these axis-cylinders are devoted to those parts of the cerebellar plate where a granular layer is lacking. We also find here in the molecular layer numerous axis cylinders of granule cells ascending and are thereby forced to the conclusion that these portions of the cerebellum are supplied by the granule cells of *other* regions.

It remains to be mentioned that the neuraxons of the granule cells on their entrance into the molecular layer appear to gain somewhat in caliber and are more thickly studded with varicosities than in the granule layer (Plate II, fig. 11). Shortly before their termination in the molecular layer they usually turn upwards abruptly and thus send their terminal arborizations to the upper portions of this layer (Plate II, fig. 12).

The "*large granule cells*" (Plate II, figs. 13, 14, Plate III, fig. 15) are, as in the other vertebrates, cells of the "*Golgi-type*," i. e. those whose axis-cylinders break up in their terminal arborizations soon after their origin. The very *voluminous cell-body* is usually round and in size often exceeds that of the Purkinje cell. The extremely coarse *protoplasmic processes* are small in number and exhibit no great tendency to branching. The nervous process arises in the majority of cases directly from the cell body, only seldom from a dendrite (Plate II, fig. 13). Its terminal arborization is less complex than in the higher vertebrates and is distributed in an entirely irregular manner among the small granule cells.

*Nerve Fibers.*

Although the course of the nervous processes of the various types of cells has already been described individually, yet it might be advisable to consider again here in particular the behavior of the neurites in their totality and mutual relations, especially as these relations are of a peculiar nature in the cerebellum of the Selachii. Besides this there are still *those axis-cylinders* to be considered *which enter the cerebellum from other parts of the central nervous system*. The presence of such nerve fibers in the cerebellum of selachians, also, is to be assumed *a priori* both from the standpoint of comparative anatomy and from the necessity that external impulses must be transmitted to the cerebellum. Notwithstanding this, the positive proof of these fibers has presented the greatest difficulty to me. After a painstaking search through my preparations, I have only been able to actually demonstrate one isolated fiber unquestionably of this kind. This one is shown in figure 16 (Plate III). We see this fiber ascend in an irregular course through the granular layer and break up in its terminal arborization in the molecular layer. This very meager demonstration of the existence of "*ascending fibers*" in the selachian cerebellum must suffice at present. In its caliber and morphological characteristics this axis-cylinder observed by me scarcely differs from that of the Purkinje cell. Nothing was observed of "*moss-like outgrowths*" at definite intervals, such as were described by Ramón y Cajal and others on the ascending fibers of Mammalia (*fibræ mousseuses*).

The tangle of nerve fibers in all layers of the cerebellar plate is infinitely complicated and it is, in fact, very difficult to find one's way. As already mentioned above, the neuraxons of the Purkinje cells, before they enter the granular layer, usually proceed a longer or shorter stretch in a horizontal direction beneath and in the layer of the Purkinje cells. In this way they form a dense nervous plexus (Plate III, fig. 17, above). This plexus is especially strongly developed where there is no granular layer under the Purkinje cells, in consequence of which *all*



the axis-cylinders are obliged to pursue their destination along the *membrana limitans interna*.

If we further consider the *granular layer*, we find here in general a dense tangle of fibers proceeding in all directions (Plate III, fig. 17); in the upper part near the layer of Purkinje cells a perpendicular direction of the fibers does indeed prevail, in the deeper layers, however, they cross each other without any order. In figure 17 (Plate III), which illustrates these relations, the delicate axis-cylinders of the granule cells are omitted; the larger fibers present come in part from the *Purkinje cells*, another part, however, undoubtedly belongs to the "*ascending fibers*." As mentioned above, there do not appear to be any characteristic marks attached to these two groups of fibers, so that they can only be distinguished by following them to their origins or to their terminal arborizations. This is, naturally, only practicable in a few fibers and in the cerebellum of selachians is especially difficult from reasons mentioned below.

The course of the fibers within the granular layer is somewhat differently arranged in those parts of the cerebellar plate where the former does not border directly upon the *membrana limitans interna*, but is separated from it by a *compact layer of medullated fibers* (the first rudiment of a central white matter) and where, besides, externally the Purkinje cells are as a rule entirely lacking so that the granular layer borders immediately upon the molecular layer, the latter being usually very thin in such places (Plate III; fig. 18). Here one sees, instead of an irregular network, well marked *fiber-bundles* at definite intervals ascending in a vertical direction within the granular layer. They stand in connection below with the basal fiber layer and extend upward to the boundary between the granular and molecular layers or also somewhat into the latter. Here they end, as though cut off, usually with a small hook-like bend. The fiber-bundles are so compact that they traverse the granular layer as completely closed masses. The axis-cylinders of the granule cells do not participate in their formation but proceed upwards between the bundles in the usual manner. They are not drawn in figure 18 (Plate III). I have unfortu-

nately not been able to ascertain with perfect certainty the further course of those fibers. Only this much is certain, that they turn in a horizontal direction along the boundary between the granular and molecular layers and proceed a distance further here in the form of isolated bundles. The roundish cross-sections of these fiber-bundles which I have met with lying at certain intervals from each other between the molecular and granular layers demonstrate this sufficiently. I conjecture that these fiber-bundles now gradually lose their individuality and finally go over into the thick nervous plexus which we saw locally so greatly developed beneath the Purkinje cells in other regions of the cerebellar cortex. I further conjecture that these bundles contain both centrifugal and centripetal fibers, i. e. both the axis-cylinders of Purkinje cells and "ascending fibers," or, in other words, all those tracts which, by means of the crura cerebelli, furnish the functional communications of the cerebellum with the other portions of the central nervous system.

Concerning the fibers of the *molecular layers*, here the ascending axis-cylinders of the small granule cells and their horizontal branches are especially prominent. The former form locally a dense forest, especially in those parts of the cerebellar plate where the Purkinje cells are lacking (Plate II, fig. 11). The axis-cylinders, as mentioned before, here increase somewhat in thickness and are quite thickly beset with varicosities. The nervous processes of the "cortical cells" also participate in the tangle of fibers in the molecular layer and likewise the terminal arborizations of the "ascending fibers," of which I have brought to view but little.

I might mention here one peculiarity which all these fibers appear to possess which pass from the granular into the molecular layer and *vice versa*. This consists in the fact that all these fibers in their passage from one layer to the other usually undergo a *double (bayonet shaped) flexure* in that they bend for a shorter or longer stretch into a horizontal direction, along this intermediate zone, and then after a second bend, about at a right angle, enter the other layer. The cause of the difficulty



with which an individual fiber can be followed from one layer to the other in *sections* is now clear from this characteristic of the neuraxons, in the transition zone the fibers usually leave the plane of the section and are thereby withdrawn from further observation. It thus comes about that we frequently see in silver preparations that the majority of the fibers ascending and descending through both layers end in the intermediate zone as though cut off, of which figures 11 and 18 (Plates II and III) furnish a clear illustration.

These observations on the arrangement and course of nerve-fibers are still of a meager nature and require much amplification by means of further investigations. The study of these relations in the cerebellum of selachians is rendered considerably more difficult and complicated through the variations in the combination of the different layers and especially through the entire absence of a granular layer in extensive regions of the cerebellar plate. The selachian cerebellum presents conditions, owing to these peculiarities, very unlike, as far as I know, the cerebella of all other vertebrates.

### *The Neuroglia.*

The neuroglia of the selachian cerebellum is in various respects, both from the morphological and phylogenetic point of view, of especial interest. The supporting substance as a whole undoubtedly stands phylogenetically on a very low scale. Sauerbeck has already succeeded in demonstrating *true ependyma cells* in the cerebellum of *Mustelus*, "*welche der membrana limitans interna ansitzen deren Fortsätze sich bis zur membrana limitans externa verfolgen lassen.*" He conjectured that they form the principal constituent of the whole supporting substance, not having succeeded in demonstrating other elements belonging to the neuroglia type. I can confirm the observation of Sauerbeck's in so far as that the *ependyma cells play a leading role in the constitution of the supporting tissue of the selachian cerebellum*; I have to add, though, that the majority of them are much modified in their morphological appearance, that they retain their connection with the *membrana limitans externa*

only in certain parts of the cerebellar plate and, furthermore, that other neuroglia elements also are present, which are probably not derived from the ependyma cells.

The *most primitive forms of ependyma cells* with an entirely embryonic habit we find along and in the immediate neighborhood of the median line of the cerebellar plate, where the median furrow nearly reaches the surface. Cells of this kind are shown in figure 19 (plate III). We see here one or two processes arise from a round-oval or triangular cell-body, which processes may again divide and extend in a fairly straight course to the surface where they lie against the limitans externa with a conical expansion. *These processes are entirely smooth.* Usually a number of processes arising from different cells are united into a thick bundle and form in this way bulky column-like structures which come out very clearly even in simply stained preparations. Not infrequently there arises also from the under pole of the cell body a short frequently branched process. Purkinje cells are not present in this portion of the cerebellar plate.

*All other ependyma cells are to be essentially distinguished from those here described, above all because most of them have completely lost their connection with the membrana limitans externa.* The few which retain a permanent connection with the surface I have found, in my preparations, almost exclusively in the thinner regions of the cerebellar plate only and especially immediately cephalad of the transition of the latter into the velum medullare posterius. Such an ependyma fiber is shown in figure 20 (plate IV). We see here the fiber arise in the typical way from a pyramidal cell body lying close against the membrana limitans interna, pursue an irregular course through granular and molecular layers and attach itself with a conical expansion to the limitans externa. On its way the fiber gives off several lateral branches which partially fall into numerous terminal twigs.

Those supporting fibers of ependymal origin which have lost their connection with the surface of the cerebellum terminate in various planes of the granular layer or reach the Purkinje cells. These elements are impregnated with extraordinary ease

and usually in great numbers so that often a dense forest of them comes into view. Figure 21 (plate IV) furnishes us an illustration of this. It shows us a closely packed multitude of fibers proceeding from the conical cell bodies on the *membrana limitans interna* and ascending in a very irregular zig-zag course in the granular layer. They are beset with numerous richly branching lateral branches which are closely interwoven with neighboring twigs and thus form an extremely delicate and complicated supporting framework, in whose meshes are found lying the nervous elements of the granular layer. At their free ends also the fibers break up in a similar manner into delicate terminal arborizations. It is striking that the fibers, where they encounter a blood vessel, frequently are closely united to the wall of the same, as illustrated in the upper left corner of figure 21. It thus appears that these fibers here enter into similar intimate relations with the blood vessels as has already been often described regarding the processes of the "astrocytes" in other vertebrates.

Where the granular layer is absent in the cerebellar plate, the ependyma fibers have a somewhat different appearance. They proceed usually more directly, have a smoother surface and give off only scattered branches during their passage through the zone of fibers. Such a fiber is shown in figure 22 (plate IV). Towards the layer of Purkinje cells we see it break up into several slender terminal branches which are distributed between the bodies of the Purkinje cells and usually end with a knob or brush-like enlargement in the vicinity of the molecular layer.

Besides the supporting fibers hitherto described of an undoubtedly ependymal origin, we find a second very characteristic kind of neuroglia elements (fig. 23, plate IV), which are confined exclusively to the molecular layer and in my opinion are to be regarded as the homologues of Bergmann's fibers in the molecular layer of the cerebellum of higher vertebrates. These fibers arise from irregular pear-shaped cell bodies lying between the Purkinje cells and extend in a tolerably direct course to the surface where they are placed against the *limitans externa* with conical enlargements. They are invested along their whole



length with a more or less dense moss-like covering which presents an uncommonly delicate aspect. They people the molecular layer in great numbers and form, when many are impregnated, an almost impenetrable thicket. These elements have in fact a great resemblance to ependyma fibers. One can imagine that these fibers have retained their original connection with the *limitans externa* and that with the progressive thickening of the cerebellar plate the cell body, released from the *limitans interna*, is gradually withdrawn into the interior of the plate. I am more inclined, however, to the view that these fibers are genetically dissimilar to the ependyma cells, that they owe their origin to a part of the derivatives of the "*germinal cells*" and are accordingly to be regarded as secondary supporting elements or as *glia elements* in a narrower sense. The same obtains for the Bergmann's fibers in general. However, as far as I know, a positive proof for this conception is not yet brought forward. Further investigations are necessary here. Should they actually prove to be true glia elements, the fibers described would represent, according to my observations at all events, the only ones of their kind in the cerebellum of selachians, inasmuch as I have not succeeded in demonstrating any elements comparable to "*astrocytes*" or "*mossy cells*" in my preparations.

It emerges from the foregoing considerations that the fundamental structure of the cerebellar cortex of the selachians as a whole shows already the typical features of that of the higher vertebrates. A lower stage of development, however, can be established in regard to the individual cellular elements, which is expressed both in the less complexity of the dendrites and axis-cylinder and in the prevailing ependymal character of the supporting structure.

*Harvard Medical School, Boston, Mass., Nov. 17, 1897.*

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## EXPLANATION OF FIGURES.

All the figures are drawn with a magnification of about 240.

*B. L.*—Basal fiber-layer.

*F. L.*—Fiber-layer (underneath the Purkinje cells).

*G. L.*—Granule layer.

*L. e.*—Limitans externa.

*L. i.*—Limitans interna.

*P. C.*—Purkinje cells.

*S. m.*—Sulcus medianus.

## PLATE I.

*Fig. 1.* Large Purkinje cells from a portion of the cerebellar plate where the granular layer is lacking.

*Fig. 2.* Small Purkinje cells.

*Figs. 3-8.* Various forms of nerve cells from the molecular layer.

## PLATE II.

*Fig. 9.* Small granule cells.

*Fig. 10.* Small granule cells; their axis-cylinders ascending between the fiber-bundles of the granular layer.

*Fig. 11.* Section through a portion of the cerebellar plate, where Purkinje cells are lacking. Compactly arranged ascending axis-cylinders from small granule cells in the molecular layer. In the granular layer a number of cells, of which the under ones send their axis-cylinders sidewise; besides these, numer-

ous axis-cylinders which partly belong to the granule cells (very delicate), partly to the Purkinje cells and are partly derived from cells lying outside the cerebellum.

*Fig. 12.* Axis-cylinders of small granule cells proceeding horizontally and their terminal arborizations in the molecular layer. Two T-shaped divisions of the ascending main fibers.

*Figs. 13-14.* Large granule cells.

#### PLATE III.

*Fig. 15.* Large granule cell.

*Fig. 16.* Ascending nerve fiber of extraneous origin and its terminal arborization in the molecular layer.

*Fig. 17.* Irregular arrangement of the nerve fibers (neurites of the Purkinje cells and "ascending fibers") in the granular layer.

*Fig. 18.* Arrangement of the nerve fibers transversing the granular layer in distinct bundles which go over into a basal fiber-layer.

*Fig. 19.* Ependyma cells from the neighborhood of the median furrow of the cerebellar plate.

#### PLATE IV.

*Fig. 20.* Modified ependyma fiber traversing the whole thickness of the cerebellar plate.

*Fig. 21.* Modified ependyma fibers in the granular layer.

*Fig. 22.* Modified ependyma fiber from a region of the cerebellar plate where the granular layer is missing. The slender terminal arborizations of the fiber penetrate between the Purkinje cells.

*Fig. 23.* Neuroglia cells of the molecular layer (Bergmann's fibers).



## PHYSIOLOGICAL COROLLARIES OF THE EQUILIBRIUM THEORY OF NERVOUS ACTION AND CONTROL.

By C. L. HERRICK.

Opportunity has afforded incidentally in connection with previous articles in this journal to point out the suggestions from anatomy in favor of a theory of nervous action based on the fundamental conception that the differentia of the various forms of nervous action consist in differences in the form of resistance and the reaction thereto, or, in other words, that nerve action partakes of the nature of equilibrium. It may now be permitted to offer fresh illustrations of the application of this principle. In the first place, however, we may note that in no department of physical science is it so plain as in neurology that we are dealing wholly with dynamic elements. While it is true that in the structure of the brain we have to do with morphological details of marvelous complexity and the descriptive side of our work is concerned with the varying outlines, sizes, and combinations of cells, fibres, etc., and the still more recondite structures within the cell and their dendrites, yet it is always obvious that these morphological peculiarities are but the expressions of inner forces and their responses to others from without. Thus it may even be doubted whether such a body as a centrosome or, at any rate, a centrosphere exists as a material element. Authors have been content to interpret the "asters" as the visual evidence of differential attraction in the cytoplasm.

It is possible to go farther and admit that all the structures with which the cytologist (and so the physiologist) has to deal are the visual interpretations of dynamic processes. This is more apparent to the neurologist than to the crystallographer

because the former grows accustomed to observe the close correlation between structural differences and conscious experience whose dynamic nature it is impossible to doubt. There can be no more doubt that the morphological peculiarities of nervous or other tissue are the expression of the equilibrated forces of growth and other functions than that the form and polariscopic qualities of a crystal represent molecular reactions. It is also apparent that the concept of matter in either case helps not at all in the explanation of these forces and that the attribute of materiality is to be determined on independent grounds. Not to discuss the ontological question at this time, it may simply be said that in our use of the morphological terms it is only with the reservation that they are convenient expressions to define the constant elements in our experience of dynamic forms. There are many advantages in this more direct interpretation of vital phenomena, for by the interpolation of imaginary material elements between the objective force and the subjective experience one loses sight of the constant dynamism—a dynamism which does not make necessary a fresh explanation of each new expression of force; for the existence of force may be regarded as self-evident when we recall that activity is the sole element of experience, and its varying forms are, in a sense, the algebraic expressions for interactions. The whole question of trophism is robbed of most of its difficulties if we think of structure as not a thing dissimilar from function, but consider both as different expressions of similar forces.

It would seem that especially in the sphere of embryology we should be ready for the abandonment of the fruitless search for material grounds for persistence of type. The theory of pangens is one illustration out of many of the absurdities to which a materialist construction is driven. The observed conformity to type observed in each of the thousand plants which may arise by minute subdivision of a moss, for example, shows how hopeless is the attempt to base on any specific material the capacity for heredity, no matter how eked out by the doctrine of latency. Correspondence in mode is the condition of identity implied by a dynamic theory, and the heterogeneity ex-

pressed in the forces of the body of a man may be expressed in the terms of the forces of a spermatozoan equally well. The assimilative power necessary when we assume that repeated nuclear division takes place without reduction of the chromatin is certainly dynamic and why should this dynamic determinant be limited to some material element? Does not the body preserve its integrity in spite of the flux of its materials? Why should not the actual material of the nucleoplasm be in a similar flux while retaining its form, i. e., its dynamic attributes?

From this point of view the coordination of parts through the nervous system becomes only a special instance of a coordination in the entire organism. It is true that even the unexpected wealth of fibrous ramification in the nervous end-organs revealed by the various applications of the Golgi method is still insufficient to explain the perfect co-adjustment of part with part in nutritive and trophic equilibrium—in fact, *any* conceivable completeness of nervous *continua* would leave something to be explained, for, in the last analysis, the processes are intracellular or even cytoplasmic. Even if we should grant that unsuspected imperfections in our present methods deprive us of the power of detecting the anastomoses between neurocytes in the same circuit, yet the most perfect conceivable continuity would still leave an appeal lying to protoplasmic transmission. A forthcoming paper will afford illustrations of what is here referred to. In the skin of many (probably all) amphibia and reptiles (*Axolotl* and *Phrynosoma*) there exists about the cells of Leydig a very complete and beautiful protoplasmic reticulum in such a way that each large cell is completely enveloped, while the meshes commingle and pass from cell to cell. This reticulum arises from certain nucleated protoblasts which are devoid of cell wall and whose naked protoplasm fills in interstices between the larger cells. This reticulum is not an artifact for it is found by the use of widely different reagents and is most complete when the fixation of the protoplasmic structure is most perfect, and in some cases of applications of chromosmic + platinic chloride + alcohol solutions this perfec-



tion leaves little to be desired. Ordinary hardening processes do not reveal the structure as a rule. It may be that the protoplasm is a delicate film which is thicker in certain parts than in others but the relation to the intercellular nuclei is certain. These are entirely distinct from the chromatophores. Bethe's methylene blue process reveals the farther fact that nerve fibers, which lose the sheaths after passing through the corium, end in knob-like tuberosities in proximity to these nuclei, though whether they penetrate the protoplasm or simply spread out upon it remains, from the nature of the method, uncertain. These nerve-fibers when stained with picro carmine or fuchsin, in contrast to haematoxylin nucleary stains, seem to blend with the protoplasm and it is difficult to decide which appearance is nearer the truth. Such close contiguity between a naked fiber and a naked protoblast is too vaguely different from continuity to require physiological separation, however important the distinction may appear morphologically.

Here we have an illustration of a condition, which I believe is more general than we now can demonstrate, in which a nervous end-organ is so connected with a meshwork of vast extent as to suggest a very extensive somatic influence of a nature similar to nervous reaction over vast tissue areas.

We venture to suggest that there is no such sharp distinction between nervous functioning and the intracellular processes of the ordinary non-nervous cell as our present terminology and usage suggest. It is certain that in the differentiation of function the cells of the body at large do not give up all of their heritage of nervous or nerve-like power. Students of histogenesis may have been puzzled, as the writer has, to account for the fact that a very remarkable degree of coordinated trophic power is exhibited by the embryonic body prior to the development of nerve tracts and end-organs. The phenomena of nervous deficiency in anencephalic monsters is equally inexplicable from the standpoint of rigid limitation of coordinating power to the nervous system. In the sponges and Cœlenterata it is plain that the coordination necessary to individual existence and perpetuation of specific characters is possible with no cen-

tral nervous system. There is a form of vital equilibrium so resident in the general system as to give rise to much the same phenomena of nervous unity as in the case of higher animals. It is not at all necessary to suppose that the cells of the body of higher animals have lost this power during the differentiation of the central system ; it would be more probable that the central system should be superadded.

There are a number of classes of cells which seem to be, in the nature of the case, freed from all direct nervous control. The chromatophores of the Amphibia, to which the writer has devoted some study, seem in some cases not to be in a direct way associated with a definite nervous supply.<sup>1</sup> They are, indeed, literary migratory, though the scope and range of movement remains to be worked out. Two things may be quite positively stated ; first, that these cells are to some extent independent of fixed nervous influence, and, second, that they are very really under indirect nervous control. Experiments tried in my laboratory many years ago showed that, in young cat fish, section of a branch of one of the cranial nerves destroyed the very marked adaptive power for the injured side. A fish, originally black, when placed in an aquarium with yellow bottom invariably changed to the color of the environment unless the mutilation described prevented it.

The observations of G. H. Parker on photometric changes in retinal pigment cells of *Palæmonetes* are interesting in this connection in showing that exposure to light causes actual changes in form and a segregation of the pigment of these cells. He finds that section of the nerve or severing the eye stalk from the body does not wholly prevent the reaction. This is an illustration of a reaction exceedingly resembling a true nervous response.

The embryonic tissues of all animals possess this coordinating sensitiveness and trophic interaction to a high degree. In the extreme case afforded by the blood corpuscles and lymphocytes it seems perfectly plain that there can be no direct

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<sup>1</sup> Methylene blue seems to show connections in some instances.

nervous relation and yet he would be a bold physiologist who would venture to deny that there is a most subtle and powerful coordination between the stationary tissues and the free corpuscles. One may talk of chemotropism or vital susceptibility, but such terms express merely the fact that the corpuscles, like other cells, are coordinated with the rest of the body and bear both its specific and individual impress. The mysteries of serum therapy only increase our confidence in such an intimate relation.

It, then, may be supposed that the circuit of nervous action in any part of the body passes through a variety of smaller somatic circuits and that the spheres of the two forms of activity overlap so that the return nerve current bears the influence of this interaction. The nervous equilibrium is only a central specialized part of a vital equilibrium embracing all the activities of the body. The wandering cell, even though not in direct continuity with a nerve fiber, nevertheless may be said to act in a "nervous field" and so is not beyond the sphere of coordination, while, on the other hand, the results of changes in the extra-nervous mechanism of the body all have their effect upon the central system. In the same way we may explain the effect of the sum of organic and total or somatic stimuli upon temperament and disposition.

The processes of nutrition may be said to be common to protoplasm quite irrespective of nervous control, but the trophic influence of the latter is well authenticated and it may be assumed that no nervous action takes place without having its effect on growth. From the above it may be gathered that the ground of the mutual reaction may be sought in the fundamental similarity of the two processes, or rather the close relation between the processes of waste and repair lying at the foundation of both. It is necessary to suppose, accordingly, that the central nervous system is continually affected by the vital phenomena of the body at large as truly as the vascular system is under the control of the nervous system.

As a striking result of this effect of the somatic or extra-neural processes, one may take the phenomena connected with



the restoration of mutilations. When the newt's foot is amputated, under favorable circumstances the organ is quickly reproduced and the parts so restored differ in no obvious way from the old organ removed. What is the power which causes such a miraculous change? Does it take place because a simulacrum of the missing limb exists in the soul and the new body develops to correspond? With due allowance for use of terms, we reply, "yes, such a simulacrum does exist." The form of the central equilibrium has been determined by constant reactions between the member and the central system and when the member is lost the equilibrium so established is still in force and the nervous stimuli which but lately served to supply tone to the limb now operate upon the stump. Intense irritation results and the tendency is to influence growth at the point of injury.<sup>1</sup> This growth is under the directive control of the nerve just as we know the normal growth constantly to be. If the nerve of the limb be injured beyond repair monstrous growth results. It may be assumed that in case the leg were amputated and the nerve destroyed in the stump above, that the efforts at restoration might be abortive or result in monstrosities. It would be well to test this matter experimentally. It is believed that the application of the ideas indicated in this paper to the higher spheres of nervous activity will prove fruitful.

Another application of the same principle is found in the processes connected with the regeneration of severed nerves. It is a well authenticated fact that, in the case of section of a peripheral nerve, the nuclei of the sheath of Schwann pass to the centre of the lumen and form the protoplasmic prota of the segments of the new nerve—a process wholly unintelligible if we agree with Kölliker in regarding the sheath nuclei as derived from non-nervous connective tissue corpuscles, but not so remarkable if the abundant evidence be accepted that these nuclei are but the diverted nuclei of the cells which formed the nerve

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<sup>1</sup> The assumption that irritation may produce proliferation is supported by the pathological karyokinesis in case of local irritation; see also processes connected with development of spermatozooids, etc.

originally by proliferation and moniliform concrescesce.<sup>1</sup> We here have an instance where the protoplasm of the cells has become specialized and the nuclei switched out of the circuit and apparently related to the process of forming the cell wall. But, in spite of the specialization implied in the production of an organ for nervous conveyance alone, it appears that the early nature of the cells is dormant rather than lost, so that in the case of injury and the consequent degeneration of the myelin and axis cylinder, the nuclei, with the small portion of less specialized protoplasm associated, return to the embryonic state and repeat the process of neuro-proliferation, after which the new channel is organized from the center outward and the nuclei return to their parietal position. It is more than probable that a similar rejuvenescence is possible in the case of other tissues also.

We have many instances of the same kind of differentiation within the cell. Take as an illustration the formation of glands in the skin of the frog, where a follicle is formed and then the several component cells are fused, the outlines being lost, and only the small nuclei which remain in the thin parietal layer of less altered protoplasm remain to indicate that the gland is really polycellular. It would be interesting in this case to institute experiments on the possibility of rejuvenescence of such cells.

In the application of the neural equilibrium theory to problems of heredity it would seem that there is a large and profitable field. Without attempting details in this direction, it may be pointed out that this point of approach renders unnecessary a vast deal of the most profitless theorizing in reference to heredity. If the neural and somatic forms of reaction are not absolutely unlike, but on the contrary are parts of a common vital type of energy (or rather force) and if it be admitted that the processes of nutrition may be and are influenced by the

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<sup>1</sup> The nuclei of the ending of the motor nerve on the muscle offer interesting collateral evidence. See the article by Dr. Huber in the last number of this Journal

neural equilibrium, it follows that the germ is also situated in the field of these equilibrated forces and its composition, i. e. its own force formula, would be the resultant of the reaction of the existing (ontogenetic) formula as modifying the earlier (phylogenetic) force formula. Instead, then, of searching for "ids," "bioplasts," "gemmules," or the like we may feel assured that, in a much more complete and integrated form, the entire life of the organism will have its effect on the germ. This confidence will not cause us to pay less attention to the structural appearance of the cell and, in particular, the germ cells, but will prevent loss of valuable effort in the invention of sterile theories and prepare the way for a dynamic interpretation of these phenomena.

It may be noted in this connection that S. Ramon y Cajal has apparently suggested, by implication at least, some of the grounds for the equilibrium theory in his suggestive article in the *Archiv f. Anatomie u. Physiologie*, 1895. He says: "Die Phänomen der vorerwähnten lawinenartigen Leitung, sowie die geringe Zahl der sensorischen Elemente (Zapfen der Fovea centralis, akustische Zellen u. s. w.) welche alle die zahlreichen Eindrücke, für welche unsere Sinne empfänglich sind, aufnehmen müssen, zwingen zu der Annahme dass jede Sinneszelle, sowie jede subordinirte Gruppe von Pyramidenzellen des Gehirns successiv an der Production verschiedener Bilder sich theiligen. Vom anatomisch-physiologischen Standpunkt aus, wird eine Wahrnehmung von einanderen, zu derselben Empfindungsquantität gehörigen, durch die Zahl und die betreffende Lage der corticalen in Erregung gesetzten Pyramidengruppen unterscheiden." It would seem to be evident from the above that not only the exact impression to be perceived is not produced by the organ of sense (since it would then be divided into a large number of parts in being transferred to the larger number of pyramid cells) but also that inasmuch as the same cells may be participants in different percepts the physiological basis for the latter must be the particular formula of these permutations in a given case and thus a simple impression must be



of the nature of an equilibrium constructed from the interactions of the cells implicated.

In conclusion, it may be noticed that the ideas advocated above have a very interesting bearing on the problem of the origin of variation. The theory of the competition of parts has taken strong hold of modern biology because it is becoming more and more evident that the sphere of natural selection must be greatly restricted and some appeal must be made to forces residing within the organism. Even Weismann in his extreme advocacy of natural selection has been forced to yield a large place to the effects of inner coordinations. We suggest that the nature of these coordinations is rendered much more intelligible by conceiving of all these vital-nutritive processes as equilibrated forces. If for any reason, a given part or tissue of the body is in the least exaggerated, its part in this complex coordination is increased and, accordingly, its reflex influence on the organism as a whole, or its nerve centers, will be increased and its quantum of the centrifugal currents will also be increased, so that the tendency will manifestly be for the newly created variation to go on increasing indefinitely until checked. The next generation will inherit this tendency and we should find that, in the absence of restraint, there would be the constant likelihood of the appearances of strange monstrosities with apparently unaccountable exaggerations of horn or spine. It requires very little familiarity with paleontology to discover that its records abound with cases in which no possible serviceability would account for the absurd burlesques which have been produced and only the comparative familiarity of existing types blinds us to the same fact. While not denying that there is a large element of useful adaptation in all cases (otherwise they would never have been preserved), yet it will be admitted that a very considerable proportion of the peculiarities and often the deeper seated characters have no such explanation. We should not be surprised at this, for it is apparent that the slightest variation not directly hurtful will tend to perpetuate itself. It may be said that all unnecessary parts will be eliminated as sapping the nutrition of the body at large. This is an

abuse of a teleological principle for it is not to be assumed that the body is reasoning from present causes to distant effects. If an eye ceases to be used it is atrophied, not because it is no longer useful and is therefore a cumbrer of the ground, but because, the function having ceased, it is actually participating less in the equilibrium than formerly and also less than other organs. But a newly formly wart on the skin may be absolutely useless, yet, like a corn, it may be the seat of irritative processes which stimulate nutrition. It is then not the ideal utility but the degree of participation in the vital equilibrium which is the primary determinant. It is necessary to seek no farther for the source of variation and it is not surprising, when we consider the infinite possibilities for the increased vital activity of one group of cells over another that natural mimicry has found at hand all the necessary variations upon which it is to work, though we must not hope to find in their number and variety the complete explanations of the imitations produced.

*University of New Mexico, Feb. 20th, 1898.*

# THE SOMATIC EQUILIBRIUM AND THE NERVE ENDINGS IN THE SKIN.

By C. L. HERRICK and G. E. COGHILL.

PART ONE.

WITH PLATES V—IX.

Few problems have proven more attractive or more illusory than the general question as to the nature of the nerve termini in the membranes, for it would seem that our concepts of the histogenesis and so of the real nature of the sense organs depend very largely upon the conclusion at which we arrive as to the relation between the various types of sensory epithelium. The senior writer suggested, in a series of papers on the brain of the lower vertebrates, reasons for believing that the first sense to come into the field of consciousness was that of smell, and a little later Edinger emphasized the same idea by his investigations of the olfactory tracts of the reptile brain. It may now be taken as fairly proven that, if the seat of consciousness is in the cerebrum, smell was the first of the special senses to find its way to recognition by it. It would then be natural that we should expect the peripheral organs of olfaction to retain a primitive character and so to afford us a clue to the early state of such organs. Then too the development of the accessory or non-nervous organs of sense has here hardly made any progress even in those most highly differentiated cases in which Jacobson's organ has assumed great proportions.

From studies of the development of the olfactory organs in reptiles, as reported briefly in earlier numbers of this Journal, the writer has been abundantly convinced of the truth of Beard's statement that the olfactory prota arise from the skin and, by a



proliferation, extend to the brain, there to enter into communication in the glomerules with the processes of the mitral cells of the tuber.

As studied in the embryos of snakes the process is as follows: The first indication of the change of the ordinary to the sensory epithelium is seen in the thickening of a portion of the superficial layer from the morphological front of the head (the region of the future infundibular recess) in relatively broad bands, one on either side of the head. As the head flexures increase, these areas are carried ventrad and come to occupy the roof of the mouth and adjacent parts of the buccal cavity. The development of the taste buds from this epithelium we have not traced in these subjects, though there is no reason to doubt that they are formed from this proton, as it is easy to see that the mucous part of the hypophysis is. At the time the first olfactory rudiments appear, the curvature is such that the hemispheres are protuberant in front and so come nearly in contact with the prota of the olfactory in the two bands of germinative epithelium above mentioned. Still there is no difficulty in seeing that the original proliferations take place in the skin and that the constant proliferation by division of the earlier cells spins the nerve fiber from the original source to the point where the tuber subsequently arises. In fact, the tuber, which has frequently been compared to the ganglion of origin of a cranial nerve, does not seem to afford origin for any centrifugal fibers whatever. In preparations by the silver method it is easy to see that the neurite of the moniliform chain of the olfactory nerve comes into relations in the glomerules with dendrites of the mitral cells. Though a considerable wealth of detail has been secured by study of Golgi preparations during the last few years, nothing has been brought to light to invalidate our original view.

For a long time during the development of the brain an obvious ganglionic mass lies below the skin at the base of the point of origin of the olfactory. The gradual elaboration of the cavities of the nares only serves to redistribute the prota without materially disturbing the simplicity of the arrangement.

In a wide range of types it has been possible to make out the adult conditions which have often been correctly described. Merkel in his classical work gives a figure of sensory endings from a cirrus of *Amphioxus* that compares in every detail with the specific cells of the olfactory epithelium of a reptile or amphibian. (Plate III, figure 10.) Few if any of those who have studied the development of the olfactory will venture to deny that the "Stiftzelle" at the peripheral end of the olfactory nerve is a member of the nervous series having the same origin, though it is doubtless conceivable that, through some strange fatality, every observer has failed to notice the intrusion of a foreign element at some stage of the process. (Fig. 31.) If, however, we take for granted that the fiber is continuous, we claim that there is an equal necessity for admitting the same for other clusters of nerve endings on the surface of the body.

Although there was for a long time considerable disagreement as to the actual connections of the olfactory nerve fibers, and the classical studies of Kölliker, Klein and Piana left the matter open, it seems as though the later studies of Ehrlich, Arnstein, Cajal, Gehucten, Retzius, Brunn and Lenhossék, who employed the silver and methylene blue methods, were sufficient to prove conclusively that the olfactory epithelium possesses rod cells whose proximal end is an actual continuity with the fiber of an olfactory nerve filament. The writer has frequently verified this in specimens of *Amphibia* double stained with hæmatoxylin and picocarmine in which very unambiguous views can be secured. A few figures from these preparations were published by Mr. Bawden, then a student in the writer's laboratory (*Jour. Comp. Neurol.* IV). Our studies in the development of the olfactory nerve show that the proton of the nerve is formed in or under the epithelium of the nasal area and that the nerve grows by moniliform concrescence of cells which arise by mitosis from this proton. From this stand-point, then, it would be expected that the neurocytes of origin would be found in the epithelium. In all essential respects the relations in Jacobson's organ are the same as in the true nasal olfactory epithelium. The accompanying figure (Plate V, Fig. 10) from an article by Lenhossék (*Anatom. Anzeiger*, VII, 19-20.) illustrates these conditions and also the fact that other nerve fibers,

apparently from the trigeminus, terminate in free arborizations between the epithelium cells. A very large following of the new school are prepared to claim that the conditions in the olfactory epithelium are peculiar to it alone and it is even attempted to correlate this with a supposed fundamental difference in origin and structure of the olfactory from all other nerves of the body. But we are able to show that in the epidermal sense buds of the tree frog and other amphibia the same continuity of nerve fiber and cell can be determined.

It has not been an altogether unnatural result of the remarkable complications of nervous structure revealed by the so-called specific methods that the results obtained by the old histological methods have been discredited and it has required some year's experience to teach us the danger of too explicit reliance on the former. Perhaps the greatest of these sources of ambiguity arises simply from the fact that has been regarded as the chief excellence of these methods, namely that the selection is so perfect that other tissues than those selected not shown at all or, even if the after-staining of sections succeeds, the conditions of impregnation are so unlike that the tracing of connections or definite relations is difficult or impossible. The absolutely contrary results of Dogiel and Cajal in the matter of the anastomoses in the retina illustrate the difficulty that exists even where the methods used are similar. The results of our own studies are rather to confirm many of the old observations and to show that there are two distinct classes of dermal endings. Of these the olfactory illustrates one and the most primitive one. In this case we have to deal with the remnants of nervous aggregates which were originally formed in or near the outer layer and in the phylogenetic development have not been diverted to a deeper level as is true in so many other instances.

In our laboratory in 1891 we made out the fact that in the oral region of the earth-worm there are cells in the skin which have a nervous nature and whose processes pass entad to the central system. Owing to a delay in the other aspects of the research the observation was not made public till



the brilliant work of Gehuchten had afforded proof of the same thing, but the suggestion was of course inevitable that we have in the lower forms a permanent retention of cells in the skin which in higher types have tended to become concentrated in the central organs. What more natural, however, than that this concentration should be incomplete, especially where these cells have acquired a specific sensory function. When the application of the Golgi and methylene blue methods revealed the fact that there is a most complicated set of free endings in the skin and that in many cases where a nervous continuity had been described there is simply a secondary apposition of a dendrite to preexisting non-nervous cells it was inevitable that the existence of cellular nerve endings should be discredited entirely. It is true that the greater part of the sensory prota are collected in the spinal and cranial ganglia and seem to proliferate thence to the periphery; but in various regions, particularly of the head, these ganglia never concentrate in a neural ridge but retain their original place in the neighborhood of pharyngeal clefts and the like and the possibility must be allowed that other cell-clusters elsewhere may have done the same. However, there is another possibility to be considered; namely, that the terminal portion of the peripherally proliferating nerve fiber may under certain circumstances develop a specialized terminal dendrite. When the nerve is in process of developing the subdivision of the distal member is repeated progressively until the definite terminus is reached and then the extreme element is charged with the function of adapting itself to the conditions there prevailing. In the case of the motor ending, even the careful researches of Huber and De Witt do not finally dispose of the question as to the origin of the end-structures. We may interpret them as follows: when the fiber reaches the muscle its terminal element, together with the nucleus, applies itself to the surface of the latter and prior to the formation of the muscle-sheath, proliferation goes on in a less regular way than during the development of the nerve itself, in this way is formed the "sole," which would, accordingly, be of a nervous nature. On the other hand, it is possible that the nerve on entering the

muscle comes in contact with a nucleus of the muscle which, under the stimulus afforded, begins to proliferate and the protoplasm of the cells so formed assumes an intermediary character and spreads out upon the surface of the muscular band as a means of applying the stimulation. To us the first is in the absence of direct evidence the more probable solution.

Observations are at hand which tend to show that extensive nervous proliferation takes place below the corium of the skin at an early stage. In section of the skin of Amphibia these proliferating cells can be seen and this is probably the origin of the ganglion plexus of the skin. (Figs. 3, 5 and 6, Plate V.)

To pass then to the nerve endings in the skin, we may first note the isolated sensory cells. These may be seen in suitably prepared sections of the head in the tree frog and other Anura and also in the neighborhood of the eye in the axolotl and other tailed Amphibia. In the tree frog, where they most numerous, these cells are grouped in threes and fours in close clustres lying in a special cavity passing through the entire thickness of the epithelial layer. The terminal segment is a slender nucleated cell, the nucleus being very narrow. The peripheral part of the cell is a narrow rod which at the periphery bears a few rigid bristles. Entally from the nucleus the cell walls are very delicate but obvious and the nerve fiber within is easily distinguishable in the doubly stained specimens. The fiber is easily followed to the corium layer and in many cases through it. It seems too that more than one nucleus can be seen in the course of the fiber before the passage through the corium. The skin is at this point very thick and the presence of large glands serves to separate the corium from the epithelial layer, so that the course of these fibers is readily followed for a long distance. In the case of certain teased preparations it was possible to isolate these fibers and study them with oil immersions and there can be no doubt as to the relations here described. So far as could be told, these fibers do not connect with the subepithelial plexus as do the fibers of the free arborizations to be described later. (Figs. 2, 12, 13, 14.) The terminal segment seems to

be entirely homologous with the segments of the nerve and its peripheral portion is perhaps simply a modified dendrite.

The endings above described must not be confused with the sense buds found elsewhere in the skin. In the latter there is a well-developed accessory apparatus in the form of the well-known beaker or "Stutz" cells, here there is simply a cavity or tube in the midst of unmodified epithelium cells. Yet it is not to be assumed without better evidence than is now at command that these two classes are of entirely distinct nature and origin. In the first place it is scarcely to be credited that two sets of sensory organs derived from the same proton and so similar in function as are the organs of smell and taste should be of an absolutely different type, and what may be said of the taste buds applies *mutatis mutandis* to the sensory buds of the skin.

The contrast between the results of different methods is nowhere better illustrated than in the different conclusions reached by Fusari and Panasci on the one hand (Arch. italiennes de Biol. XIV, p. 240) and those of Arnstein (Archiv f. mikroskop. Anat. XXXXI, 2). The former authors worked with the chrome-silver method and describe a direct communication of the nerve fiber with the axial (rod) cells of the taste buds. (This we are able to substantiate from personal observation.) Arnstein, on the other hand, denies such connection most emphatically and claims that teased preparations with methylene blue show with all possible clearness that there is no such connection, but instead that the varicose nerve fibers form a felt-ing of fibers around the axial and outer cells of the bud and end free in the pore. Arnstein finds quite similar nerve endings in the filiform papillæ. He does not find forked cells, but inclines to the view that such cells result from the separation of the true nerve fiber from the peripheral end of the cell to which it is attached. The appearance of continuity between the cell and the nerve fiber is said to be illusory and is explained as due to the blackening of the cell as well as the fiber. Ehrlich (Deutsch. med. Wochenschrift, 1886, 4) described intensely colored cells in the mucous membrane of the olfactory region which pass without interruption into a nerve fiber, but these cases Arnstein also dismisses as illusory. Dr. Niernack has also reached similar conclusions by the use of different material (Anat. Heften, Merkel und Bonnet, Anat. Anzeiger, VIII, p. 20.)



Inasmuch as the epithelial layers of the mouth and tongue are morphologically only portions of the skin, it is necessary to examine these regions for light on the nerve endings as they may be modified under the special conditions here existing. In the frog, which has been the subject of the most elaborate investigation, the sense of taste cannot be at all highly developed, for the animal is accustomed to swallow its food, chiefly horny coated insects, without mastication; and experiments (Bethe) prove a very sluggish response to chemical irritants. In the tongue of the frog, as well as in the palate, there are numerous scattered specific sense organs, those of the tongue being flat end-plates, while those of the palate are protuberant sensory papillae. Although these organs were described by Leydig in 1858 they have frequently been the objects of special study since then and even now authors are not wholly in agreement as to the details of the structure. The cellular elements in these sense organs consist of the cylinder of flask cells forming the protection for the sensory rod cells, a subordinate variety of which has been termed forked cells by reason of the divided peripheral projection. Alate, or winged cells, around the cup or flask have also been noticed by some authors. Bethe, who has recently studied these buds by means of the modification of the methylene blue method which bears his name, finds two sorts of nervous termini in them: first, free termini lying between the cylinder cells and reaching the surface, second termini with bulb-like expansions on various cells. (Fig. 8.) One type of such endings is three-lobed and such endings are affixed to the sides of the cylinder cells; the other variety has simple circular end-plates and these endings are found on the rod cells, fork-cells and possibly also on cylinder cells. In no case did Bethe succeed in finding actual continuity between the rod-cells and the nerve. He in fact seems to find greater intimacy of connection between the cylinder cells, which are not supposed to have a nervous function, than with the rod-cells and in no case is there more than a contact with the cell wall. He explains the continuity detected by Arnstein and others as the result of faulty observation and imperfect methods. In the ordinary pavement epithelium of the palate Bethe finds termini on gland cells and ciliated cells, as well as deeper elements. It should be noted that the finding of the three-lobed end-plates on the cylinder cells was not a uniform occurrence but rather exceptional and the suggestion is near that this is the result of an accidental state of the fibers and not a natural or permanent organ.

Our own studies of the gustatory epithelium of the axolotl are in accord with the results of Bethe upon the frog so far as the diffuse endings are concerned, though the methylene blue does not give adequate insight into the connections between fibers and cells. The taste buds, on the other hand, afford similar results to those obtained from the sensory buds of the skin. The source of many of the erroneous conclusions reached is, as mentioned beyond, the fact that in successful methylene blue preparations it often happens that fibrous elements stain when the cells of origin for the same fibers do not.

*Diffuse Peripheral Connections.*—Various early writers have reported the existence of a dense net-work or felting of nervous material among the epithelial and even the corneum cells of the skin. This structure was first made out by the use of gold chloride and there was always left open the possibility that the appearance was due to the disposition of metallic salts in the interstices between the cells. Dogiel in his paper on the nerve endings of the genitalia figures a very extensive mesh-work of this kind with here and there a free knob-like termination and he traces the lower part of the reticulum to a direct communication with a set of nerve fibers passing perpendicular to the skin. (Fig. 1.) Strong in his paper on the cranial nerves of the frog figures a similarly minute meshwork which is revealed in this case by the use of the Golgi method. In all of the above cases there is the element of uncertainty growing out of the fact that the methods are impregnation rather than staining processes and are histologically uncertain. It would then be eminently desirable to supplement the evidence from these sources by other means. In the study of the skin of the Amphibia it is easily noted that there exists at the base or ental aspect of the layer of Malpighi a layer or stratum which is in a peculiarly nascent state. These cells are devoid of the thick and rigid walls characteristic of the superficial cells and are protoblasts rather than complete cells. In this layer we may find, at all stages, the evidences of mitotic division. In fact there is a permanent proliferating zone in this region. Comparison of this stratum with that of higher vertebrates shows that the latter form

no exception, though it is not always easy to detect the protoblastic elements. A single theoretical consideration is sufficient to convince one that this is what should be expected, for it is of course recognized that every type of vertebrate has some provision for the constant or occasional removal of the skin. In some cases the process of removal of the corneum is intermittent, while in others it is gradual. In either case it is obvious that there must be a proton of undifferentiated material—of cells that have not passed beyond the plastic stage. In those parts of the skin where there is little differentiation between the various layers the difference between the corneum and deeper cells is not readily detected in preparations by the usual processes, but in the thicker portions where the so-called Leydig cells appear the basal protoblasts are crowded into the interspaces and pried apart. One effect of this process has been to stretch the connecting protoplasm into an excessively thin layer or film enveloping the Leydig cell either completely or as a coarse mesh-work of naked protoplasm. In all the preparations we have seen, even those in which the preservation has been as perfect as possible, without the least evidence of shrinkage, the appearance is that of a broad reticulum arising in the intercalary or basal protoblasts and enveloping the cell in such a way as to wrap it completely in the products of the adjacent protoblasts. The most perfect process of preservation for such structures is a combination of chrom-acetic and platinic chloride diluted in alcohol. The use of Merkel's solution also gave very good results, while the various osmic acid solutions invariably produce too great shrinkage of some parts, especially of the reticulum. In the first mentioned solution it appears that the natural tendencies of the alcohol and the chromic acid counteract each other while the fixing action of the platinic chloride is in no way interfered with. The avidity to all the usual stains after this treatment is also very great, while in the osmic preparations there is not only general diminution of the receptivity, but, what is worse, the effect is not uniform even in the same class of tissue in the same preparation. In properly prepared sections the reticular structure of the protoplasm of the Leydig



cells is most beautiful, but when osmic solutions are used the contents of the vesicles is blackened and the result is a granular appearance instead. The pericellular mesh-work is stained red by picrocarmine, as is all protoplasmic matter, while the nuclei are all selected by the hæmatoxylin. Nerve fibers stain red but their nuclei are purple. The nerve supply is abundant and the fibers can be traced without difficulty through the corium layer in all preparations. The sheaths seem to cease after passing the corium and the subsequent course is less easy to make out. In a considerable number of cases it has been possible to trace such fibers with all desirable clearness to actual connection with the bases of the lower protoblasts above mentioned. The fiber is red, as is the protoplasm, so that it remains possible that the exact nature of the union is not obvious, yet from the fact that two masses of naked protoplasm thus come in contact, the range for possible modes of union cannot be extensive. In any case the most careful examination under immersion lenses of well-stained specimens does not reveal any form of intermedation between the fiber and the protoplasm of the cell. Nor is this relation limited to the lowest layer of protoblasts alone, for it is possible to trace fibers to some of the higher members as well. The attempt has repeatedly been made to count the number of fibers entering the given area and then to compare this number with the number of protoblasts in the same area, with the result that the fibers proved more numerous than the cells in the lower series, thus offering independent evidence to the effect that these fibers are destined to more than the single basal row of protoblasts.

The pericellular net-work has been described by a number of the earlier observers, but in each case the real nature of the structure has not been detected. Paulicki and Pfitzner both regarded it as a mesh-like thickening of the cell wall. The latter thinks these "ribs" serve for the point of attachment of the "intercellular bridges." Part of Paulicki's description is given in full. "An einigen Leydig'schen Zellen wurde ich auf kleine kreisförmige, länzende, dunkelconturirte Figuren aufmerksam, die in ziemlich regelmässigen Abständen von einander entfernt

der äusseren Fläche der Zellmembran aufpassen. Es stellte sich nun alsbald heraus, dass dieser Befund bei allen Leydig'schen Zellen ein ganz constanter ist. Ueber die Deutung dieser Gebilde erhielt ich durch Zellen, wie deren mehrere abgebildet sind, Aufschluss. Hier fand sich ein doppeltconturirtes Gitterwerk, welches über die Protoplasmakörner hinwegging. Die Balken des Gitterwerks theilten sich öfters gabelförmig und waren bald dünner, bald dicker. Es ist nun anzunehmen, dass das Gitterwerk hervorgebracht wird durch rippenartige, partielle Verdickungen der Zellmembran, und dass bei solchen Zellen, wo ein derartiges Gitterwerk zu sehen ist, der Schnitt die Zelle tangential getroffen hat, während bei den Zellen, die dieses Gitterwerk nicht zeigen, die dagegen in der Zellmembran von Streck zu Streck kleine, glänzenden Ringe besitzen, der Schnitt mitten durch die Zelle gegangen ist. Die kleinen Kreise, die der Zellmembran aufsitzen, stellen die Querschnitte der rippenartigen Verdickungen der Membran dar. Die rippenartigen Verdickungen der Zellmembran zeigen sich durchs ämmtliche Farbestoffe ebenso gefärbt, wie das Protoplasma, weshalb sie leicht übersehen werden können." The author also notices that these bands are sometimes sharply stained by fuchsin, a fact that, in connection with the above, might well have suggested that these supposed ridges on the cell wall have a nature more in common with that of protoplasm. Still more suggestive was the additional observation that these ridges are not limited to any single cell, but often pass to neighboring cells without interruption. He says "Ich sah, dass die Balken von einer Leydig'scher Zelle continuirlich zusammenhängen mit den Balken benachbarter Leydig'scher Zellen, dass ein zusammenhängendes Balkenwerk sich über mehrere Leydig'sche Zellen ausdehnte. Ausserdem sah ich aber auch, dass ganz ähnlich gestaltete Balken sich auf die benachbarten Epithelzellen fortsetzen."

Our observations leave no doubt that this meshwork is not only of a protoplasmic nature but that the meshes are connected with the nuclei of the basal and intercalary series. (Figs. 17-20). It is easy to trace the meshes into communication with the protoplasm surrounding these protoblasts. It is more difficult, ex-

cept in the case of perfectly preserved material, to follow the nerve fibers to the bases of the cells of the higher series, i. e., those about the sides and ectad of the Leydig cells. In good methylene blue specimens stained *intra vitam* (Figs. 21-23), the fibers can be traced for a considerable distance into the epithelial layer among the intercallary nuclei, but it is only in specimens stained with picrocarmine and hæmatoxylin that the actual connection with the cells can be made out. Even here the question (always left wholly undecided by the methylene blue method) as to the nature of the association is not entirely deprived of its ambiguity. When a fiber of naked nerve-plasm unites with a protoblast of naked cytoplasm, who shall say whether the connection is primary or secondary in the absence of the most intimate embryological evidence or regeneration experiments?

An important question in this connection is that as to the source of the nerve fibers. Do they arise in the prota of the skin or do they enter the skin from out-growths of the spinal ganglia? It would seem natural to conclude that the latter is the case, and yet it is not a little puzzling to see that nearly every cell in this series has its fiber. Then, too, the fact has been repeatedly observed that the protoblasts are continually dividing, even in rather large specimens of axolotl. (Fig. 20). It must be left to careful embryological studies to decide whether there are cells of origin in the skin for centripetal nerves or not. Another question must await either an embryological or pathological solution, and that is the detection of centrifugal fibers among those entering the skin. Such non-medullated fibers doubtless occur and we may think of the plexus immediately below the epithelium is the probable site.

We have sought to verify the results above described by the application of the methylene blue *intra vitam* method as well as the tissue methods used by Dogiel, Bethe and Huber. Making all due allowance for the ambiguity of these methods, it seems that the results are in harmony with those above mentioned. It is not difficult to secure impregnations in which every fiber is stained throughout its course through the corium,



but to our surprise they seemed to stop short in the vast majority of cases in the zone at the base of the layer of protoblasts, while only in comparatively few cases did we trace connections like those described by Bethe with cells of higher layers. In the chromatophore zone just ectad of the corium in many parts of the skin it was possible to trace fibers horizontally long distances and in some cases supposed communications with the chromatophores or similar bodies were noted. (Fig. 21). In most cases these cells were nearly destitute of pigment and pass by all gradations into undoubted ganglion cells.

In this connection mention should be made of the remarkable results reported by Dr. W. Pfitzner.<sup>1</sup> This writer claims to trace the fibers after their passage through the corium into the substance of the cells and to follow them to small knob-like endings free in the protoplasm of the cells. More than this, he traces to each cell, not only of the deeper layers but also of the stratum corneum, two independent fibers from quite distinct sources and founds upon this observation an elaborate hypothesis, which unfortunately is deprived of all standing-room by the evidence now at hand. Mr. Massie has pointed out that there is a stage in the young amphibian skin when a curious skein of a material staining deeply with some reagents is found in the cells. The senior writer, who made the preparations used by Mr. Massie, can vouch for the accuracy of this observation. It is not unlikely that the suggestion is warranted that this skein is an embryonic and transitory element in the development of gland cells, as it is not found in all the cells but in a certain class dispersed among narrower cells having a different reaction. This skein (Fig. 4) is as certainly intracellular as the nerve fibers are extracellular in their course. Figures almost identical with those published by Pfitzner as the results of his observation can be secured by his methods, especially if the sections are taken a little oblique (Fig. 24.) The process serves to stain very distinctly the part of the nerve that is medullated, i. e. that part extending through the corium, but not that part which extends

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<sup>1</sup> Nervenengungen im Epithel. *Morphol. Jahrbuch*, 1882, p. 726.

above the corium among the cells. Such fibers can be seen, it is true, but they are so different in appearance from the medullated part of these fibers that we are forced to conclude that what Dr. Pfitzner really saw is the intracellular skein of which mention has been made. It is a most natural mistake in the absence of more reliable methods and especially as the methylene blue process was not at his disposal. The finding of two nerve termini in each cell is apparently to be explained as a result of the fact that the base of the skein is hidden, as we found it to be in oblique or thick sections, so that the appearance figured by Pfitzner frequently recurs and if one had a preconception in favor of the nervous structure of the element one might easily construe it as he has done. After the above we may be released from the obligation to consider the extensive and interesting theories based upon the supposed intracellular endings.

*Transitional Cells.* In certain regions of the skin the epithelium layer is greatly thickened and the Leydig cells are reduced in number or carried to a higher (ectal) level. In such portions of the skin, as on the dorsal region, an interesting modification of the structure above described is found. Here the lower series of cells is elongated in a direction perpendicular to the surface forming a sort of palisade type of cells. A definite wall is often apparent in the lower portion proximad of the nucleus, while the peripheral part seems to fray out into a representative of the pericellular mesh-work. Where the Leydig cells are present there is every reason to believe that these cells participate in the formation of such of a pericellular network as has been described above but somewhat modified by the changed conditions. In a large number of cases we have observed a nerve fiber after passing through the corium seeking the base of these cells and making an intimate connection with one of them. Here the opportunity to observe the union is much better than the other case and the connection is perfect. In a certain sense these cells are intermediate between the rod cells and those that supply the pericellular meshwork. (Fig. 25.)

Dogiel<sup>1</sup> has shown that in the eyelids of man, for example, where the number and complexity of the sense organs is extreme, the terminal bodies consist of a covering of several connective tissue layers separated by zones of flat epithelial cells enclosing the nerve net. The nerve net is described as lying free in the interior of the bulb, though a faintly stained material was noticed and regarded as coagulated lymph which may represent cellular elements not competent to be revealed by the methylene blue method. (Fig. 9.) The nerve fiber loses its sheath before it penetrates the bulb and at once divides into spirals or coils forming a loose mesh-work. Aside from these specific cells, there are extensive arborizations and nets of fibers diffusely scattered in the epithelium at large.

In some respects the fullest description of the highly differentiated sense organs of the skin of the genitalia has been given by Dogiel and his results are pertinent to our purpose, inasmuch as he finds that all the end-organs reduce to one type—a terminal reticulum. The so-called genital sense organs and the Krause's and Meissner's bodies all prove to consist of a capsule containing a reticulum of varicose fibers and, especially in the case of the genital corpuscles, those of the same order are frequently connected by lateral anastomoses. In addition to these special organs, Dogiel traces medullated fibers into an inter-cellular reticulum within the epithelium so fine and dense as to come apparently into relations with all the cells of the deeper parts of this layer. Occasionally a branch turns peripherally and ends in a knob at some distance below the surface. We seem, then, to have evidence that the typical form of nerve ending is a close pericellular network, though Dogiel's method is not such as to allow of determining the relation of the fibers to the cells. (Fig. 1.)

The most remarkable suggestion respecting the homologies of the sense organs of the skin in amphibians is that of Maurer who thinks that the hair of vertebrates can be traced back phy-

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<sup>1</sup> A. S. DOGIEL. Die Nervenendigungen i. Lidrande, etc. Archiv f. Mik. Anatomie, XLIV, 1, 1894.



logenetically to these sense organs. Leydig in *Biolog. Centralblatt*, XIII, scouts this idea and derives the hair from the so-called "Perlorgan" of certain fishes. The resemblance and affinity of the sense organs is rather with the auditory apparatus, as shown by Ayers and others.

*The Sense Buds.* It is interesting to observe the wide differences of opinion of competent observers as to the endings in the end buds. Lenhossék (*Anat. Anzeiger*, VIII, 4) denies absolutely Fusari and Panisci's statement that the proximal extremity of the sensory cells in the taste bud passes directly into a nerve fiber and states that the nerves always end free in the bud, or rather form a meshwork surrounding it, thus constituting a peri-gemmal reticulum. Nerve fibers pass in a horizontal course below the epithelium and give off collaterals from time to time which form a felting of free fibers among the general epithelium cells. Essentially similar conditions prevail in the sense buds of the mouth of fishes and the author concludes that the rod cells are to be considered as short apolar nerve-cells and that the class of nerve endings found in the earth-worm is found in vertebrates only in the olfactory organ. (Figs. 15 and 16.) Retzius takes the same view, but finds that the nerve fibers are not perigemmal but intragemmal, thus illustrating the difficulties growing out of a reliance on the Golgi and methylene blue methods alone.

A. Geberg in a brief article in the *Anat. Anzeiger*, VIII, I, claims to be able to demonstrate the endings of the auditory nerve in the cochlea by the methylene method, but, inasmuch as the tissues were not stained, it seems that his conclusion, that the fibers attach themselves to the hair cells without communicating with the latter, must be considered as non-conclusive.

Having reinvestigated the nerve endings in the sensory buds of the skin of the axolotl with material leaving little to be desired as to the fixation and hardening, and which had been double stained successfully, we are able to assert with great confidence that, in this case, there is a special cellular nerve terminus having a direct basal connection with a nerve fiber. The nucleus of these cells (which cannot be termed appropriately

rod cells or "Stiftzelle") is narrower and more deeply stained than the supporting cells and occupies the entire width of the cell. The peripheral part of these cells has not been correctly described as yet. In reality it consists of a projection of the cell walls to form a narrow tube. These walls are delicate and very thin but easily seen because of the contrast with the protoplasmic fiber contained in it. The latter structure is delicate but stains a deep red with the picrocarmine, while the walls are not stained by that reagent. (Figs. 26-30.) This axial fiber differs not at all from that seen in the clusters found in the scattered sense organs on the head of the tree frog and the frog. (Fig. 32.) The proximal portion of the cell is not as easy to trace, for the corium and often the chromatophores obscure the connections to a degree. Yet it now and then happens that the direct communication with a nerve fiber rising through the corium can be made out. Of course it may be insisted that this connection is only a secondary one, but nothing but evidence from embryology or degeneration experiments will substantiate or refute the claim. So far as the evidence now goes, the scattered cells above mentioned and those in the buds stand or fall together, and for the former the evidence of direct continuity between cell and nerve is unimpeachable.

*The Plexus Beneath the Corium.*—In portions of the skin stained *intra vitam* by the methylene blue method and examined at once in glycerine very perfect views of the marvelously elaborate plexus beneath the corium can be gained. The fibers are of two sorts, the larger being connected with the fibers from the nerve bundles from the central system, while a part at least of the fibers of smaller calibre have a local origin in certain ganglion cells of this region. These cells were first detected in preparations double-stained with hæmatoxylin and picrocarmine and were seen in section in a plane parallel to the surface. In the methylene blue preparations they are very conspicuous and surprisingly numerous. The nuclei are large, while the protoplasm of the cell does not stain or only slightly with the blue. It is an interesting and most instructive fact that the cell body remains transparent, while its own neurite or axis cylinder pro-

cess is mostly intensely stained through its entire length. The hiatus between the fiber and its cell is slight but sufficient to cast a doubt on the fact of communication were the conditions not absolutely favorable. With a high power it is possible to see the sheath and the faintly tinged protoplasm so that no doubt is in this case possible.

It may be noted also that other methods seem to show that it is entirely possible for the protoplasm of a cell to react differently from that of the axis cylinder derived from it. Thus may be explained many of the ambiguous and conflicting results of the applications of the methylene blue process. Fig. 33 illustrates the appearance of a section stained with hæmatoxylin and picrocarmine, while Fig. 23 is from a methylene blue preparation. Figs. 33-37 are from surface views of the plexus, showing the ganglion cells. Figs. 38 and 39 are from the same region, showing connections with vessels and chromatophores (Fig. 3.)

It will be seen that the fibers of this plexus below the corium are of two sorts. The fine fibers arise, in part at least, in the local ganglion cells and can be traced to the nerve bundles, which they enter and then mingle with the fibers of the larger sort. In the perpendicular sections it is easy to see that a certain number of fibers from the general "mixed" nerves pass without interruption into the skin and so do not participate in the formation of the plexus. Others, on the other hand, divide dichotomously in the level of the plexus and the branches give off "collaterals" that pass through the corium and so reach the epithelial layer. It is not possible to state positively that fibers from the ganglion cells of the plexus give off fibers to the skin, though such certainly is the appearance. After passing through the corium, the fibers do not all at once seek out their definite termini in the cells of the epithelial layer, but they often turn sharply at right angles at the ectal surface of the corium and pass long distances parallel to the surface. This tendency is more marked in some regions than in others. This fact greatly complicates the study of the endings. In the case of taste buds and the organs of the lateral line this is one of the most serious dif-



faculties in the way of a correct interpretation of the appearances presented by sections.

A discussion of the theoretical bearings of these facts and further details must be deferred to the second part of this paper.

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Since writing the above we have been able to settle several points previously in doubt. None of our preparations of the skin of amphibians gave unambiguous results for the glands of the skin. We have at last succeeded in securing excellent *intra vitam* impregnations in the toad (*Bufo* sp.) in which it is easy to trace the non-medulated fibers from the plexus ectad of the corium, and also from that entad of it, into the most intimate connection with the superficial walls of the glands, which in this species are very large and highly functional. The fibers are of small caliber but are excessively numerous and envelop the whole gland in what at first looks like a closely woven reticulum, but a close study shows that the appearance of a reticulum is due to the repeated dichotomous branching of a large number of distinct nerve fibers. These fibers cross at slightly different levels and there is no doubt in most cases of the complete distinctness of the fibers as they cross. Upon these fibers are frequent varicosities which may be due to imperfections of the process or may be the points of attachment of the fibers upon the cells of the gland. Of course this method does not admit of determining the exact relation of the nodosities to the several cells, but there can be no doubt of the existence of a very intimate and necessary connection. One is forcibly struck by the close resemblance of this periglandular felting to the perigemular reticulum described by many authors in the case of the sense buds. The latter is, as we have before insisted, entirely distinct from and totally unlike the intragemular endings in distinct cells which may be demonstrated by a wide range of independent methods.

The same preparations used in the earlier parts of this paper have also afforded to a more extended study a number of satisfactory views of the connection of the ganglion cells of the

reticulum below the corium with fibers—not only with such as pass directly into the nerve bundles but, as we now find, with with non-medullated fibers which pass through the corium and end in relation with the cells of the epithelium layer. We also find that these and other fibers, after passing through the corium, turn and pass for long distances parallel to the surface to their final destination in the upper layer. This seems to be particularly true of the fibers of the perigemmular series of the sense buds. In some cases well defined bundles of nerves in a common sheath pass through the corium, while in those cases where the nerve sheath is present it is soon lost after passing the corium. It seems natural to conclude that the non-medullated fibers of the epithelium are essentially similar to the fibers of the same structure that supply the glands. If so, we may add that these are in both cases centrifugal and we have a suggestion at least toward the solution of the puzzle as to the respective functions of the several classes of fibers. That the general cells of the skin have more or less power of absorption and excretion, as well as secretion, can hardly be doubted and, if so, why may not these fibers from the disperse ganglia of the peripheral sympathetic system be the neural sponsors for these functions? The methylene blue method reveals the same sensory endings in the skin that we have described fully from histological preparations, but curiously enough they appear as fibers simply because the nuclei are not stained and this fact explains the discrepancy in the two methods.

It is interesting to compare the intercellular net-work described above with the similar so-called connective tissue net-work described by Bruyne (*Arch. de Biol.*, XII, 1892) surrounding the muscle fibers. The figure given in the article by the same author in *Anat. Anzeiger*, X, 18, is so remarkably similar to the appearance we have called attention to that one may be pardoned for suspecting similarity of nature. It may be that more than one instance of intercellular bridges rests on the misinterpretation of similar structures. The relation of the space so kept open between the cells to the circulatory fluid is a question of greater interest than seems to have been suspected.

NOTE ON THE METHYLENE BLUE PROCESS. It appears that we have had in one respect the usual experience with the methylene blue *intra vitam* impregnation process. It is not difficult to secure excellent impregnations of the nerves of the skin of the Amphibia in which the nerve fibers are deeply and quite selectively stained, yet it appears that there is a strong tendency for the stain to be extracted or rendered diffuse by the process of imbedding so that tissues which were very perfectly stained in the glycerine are quite unsatisfactory in thin section. It appears that the difficulty is in the action of the alcohol, which is required in both the paraffin and the celloidin methods of imbedding. To obviate this difficulty we have resorted with good results to the use of a mixture of gum arabic and glycerine. The fragment is placed in glycerine or may be placed at once in the gum-glycerine. After an impregnation of a day or two in a closed bottle the specimen is mounted in a paper tray with the mixture and the latter is allowed to evaporate till a consistency is reached which will permit it being placed in the microtome and sectioned. In this way sections are secured thin enough to serve the purpose desired and these may be mounted in gum-glycerine or may then be dissolved out of the gum and treated in any way desired.



## EXPLANATION OF FIGURES.

## PLATE V.

- Fig. 1.* Diagram of the skin of the sexual organs, after Dogiel.  
*Fig. 2.* End-organs in the skin of the tree frog, original. Teased preparation.  
*Fig. 3.* Sense bud of young salamander. Original.  
*Fig. 4.* Skin of tadpole with nerve endings and the transitory skeins interpreted as nerve endings by Pfitzner.  
*Fig. 5.* Skin of very young tadpole. Original.  
*Fig. 6.* Skin of tadpole, near angle of mouth, Original.  
*Fig. 7.* Sense bud of *Amblystoma*. Original.  
*Fig. 8.* Nerve endings in the epithelium of the frog, according to Bethe.  
*A.*—"Gabelzelle," from sensory papillæ of tongue.  
*B.*—Cylinder cells.  
*C.*—Isolated rod cell.  
*D.*—Upper part of papilla.  
*E.*—Ciliate cell of palate.  
*Fig. 9.* Nerve ending in the human conjunctiva. Dogiel.  
*Fig. 10.* Nerve endings in Jacobson's organ. Lenhossék.  
*Fig. 11.* Nerve endings in the taste buds. Arnstein.

## PLATE VI.

- Fig. 12.* Section from the skin of the head of a tree-toad. *a*, nerve bundle and endings; *b*, gland; *c*, corium; *d*, small gland; *e*, chromatophore.  
*Fig. 13.* Skin of head of leopard frog showing cellular nerve endings in groups penetrating the skin.  
*Fig. 14.* Similar endings from the tree frog.  
*Figs. 15, 16.* See Plate VIII.  
*Fig. 17.* Part of the skin of the axolotl showing the nerve bundle on its way to the skin and the pericellular net-work.  
*Fig. 18.* Skin of axolotl showing pericellular net-work and the nerve-fibers entering from below.  
*Fig. 19.* Similar section fixed in Flemming's solution.  
*Fig. 20.* A section of portion of axolotl skin where the Leydig cells (*L. c.*) are two-layered. Proliferating cells (*b*) in lower series of protoblasts; *c*, corium; *B. V.*, capillary; nerve fibers entering from below.  
*Figs. 21-23.* See Plate VIII.  
*Fig. 24.* Skin of tadpole as figured by Pfitzner.

## PLATE VII.

*Fig. 25.* Section from a different part of the skin with cellular nerve termini. This is probably to be explained as the result of the elongation of the basal series of the epithelial cells.

*Fig. 26.* Sensory bud from skin of axolotl, showing the tubular peripheral ending of sensory cells with fine thread of protoplasm extending to periphery and the basal connective with nerves.

*Fig. 27.* Sensory bud from another part of skin.

*Fig. 28.* Similar bud in which the peripheral portion of the sensory element seems divided. Explained as due to the shrinkage and "fraying out" of the wall.

*Fig. 29.* See Plate VIII.

*Fig. 30.* Isolated supporting cells from specimens similar to Fig. 28, stained with hæmatoxylin, picro-carmin and methylene blue. Are the blue fibers nerves, or are they lines of precipitation in folds of the cell wall due to shrinkage? Compare Fig. 11.

*Fig. 31.* Cells from nasal cavity of leopard frog.

*Fig. 32.* Nerve endings from skin of same to illustrate similarity to the last.

*Fig. 33.* Skin of gills of axolotl to show ganglion cells beneath the corium.

## PLATE VIII.

*Fig. 15.* Pericellular nerve fibers from sensory bud of conger eel.

*Fig. 16.* Intrabulbar endings in *Barbus*. (Both 15 and 16 from Lenhossèk.)

*Fig. 21.* Skin of the axolotl showing nerve endings in or near the chromatophores and in the skin of the axolotl. Methylene blue.

*Fig. 22.* Similar to Fig. 21, showing endings in layer of protoblasts.

*Fig. 23.* Perpendicular section through skin of axolotl stained *intra vitam* with methylene blue and cleared in glycerine. The plexus beneath the corium is clearly visible.

*Fig. 29.* Cells similar to to Fig. 28, stained with methylene blue.

*Fig. 34.* Surface view of methylene blue preparation, similar to Fig. 33, showing connection of ganglion cells with nerve bundles.

*Fig. 35.* Same as Fig. 34.

*Figs. 36, 37.* Ganglion cells of large ramose form from same layer as above.

*Fig. 38.* Relation of nervous reticulum below the corium to the capillaries.

*Fig. 39.* Chromatophore-like ganglion cells.

## PLATE IX.

*Fig. 40.* Section of the skin of the head of a toad (*Bufo*) after *intra vitam* injection with methylene blue and fixation with Bethe's solution of molybdate of ammonia. Examined in glycerine. The section is somewhat oblique so that the duct and part of the body of the gland is removed. The delicate non-medulated fibers are seen generously distributed over the uncut surface of the gland. Coarser fibers are also seen in the lower and upper plexuses, also a bundle of sensory rods at the left.

*Fig. 41.* *Intra vitam* methylene blue preparation of skin of axolotl, showing connection of cells of the ganglionic meshwork beneath the corium with the epidermis. *a*, fiber passing to cells of the intracellular reticulum; *b*, non-medulated fibers from a nerve piercing the corium; *c*, *c*<sup>1</sup> *c*<sup>2</sup> and *c*<sup>3</sup>, ganglion cells of the plexus beneath the corium.



THE BRAIN OF THE FUR SEAL, CALLORHINUS  
 URSINUS; WITH A COMPARATIVE DESCRIPTION  
 OF THOSE OF ZALOPHUS CALIFORNIANUS,  
 PHOCA VITULINA, URSUS AMERICANUS  
 AND MONACHUS TROPICALIS.\*

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WITH PLATES X TO XIII.

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\*This article was written at the request of a member of the Bering Sea Commission and will appear in their Report of the Bering Sea Fur Seal Investigations,

## INTRODUCTION.

The specimen was from a young male pup twenty five inches in length, weighing about twelve pounds. The brain was still incased in the dura and on the basal surface portions of the cranial bones were left adherent to this membrane. An occasional cut through the dura caused a protrusion or hernia of the cerebral substance.

The weight of the brain in the fresh condition, as reported by Mr. Lucas, was ten ounces and two hundred and forty grains. This included the dura with the attached cranial fragments.

The specimen was preserved in a "rather strong solution of formalin" and except for some swelling of the tissue and softening of the interior was in a very good condition. The bloating was indicated by the increased weight which, immediatly after the receipt of the specimen, Dec. 12, '96 was found to be 13 ounces, a gain of nearly three ounces, by the closure of the fissures and by the cerebral hernias. The weight without dura and attached fragments of cranial bones after preservation from Sep. 1 to Dec. 12 was  $9\frac{1}{2}$  ounces and 80 grains (avoir.). The lateral girth was 26 centimeters, the longitudinal girth with the oblongata cut off at an even level with the caudal surface of the cerebellum was 24 centimeters, being slightly less than the former. This may, perhaps, be accounted for, to some extent, by the tape resting slightly in the inter-cerebral cleft, and to the bloating, as this would affect the lateral rather than the longitudinal circumference.

The brain as indicated by the girth measurements was of a subglobular form slightly tapering at the ends and its outer substance though firm was not unyielding. Twenty four hours immersion in 95% alcohol served to contract the nervous tissue sufficiently to open the fissures and yet to retain enough flexibility of their walls to permit of an easy examination of their

depths. In order to obtain the desired results, after photographing the dorsal and ventral surfaces of the entire brain, it was cut across and the crura cerebri or mesencephal, and the cerebellum and oblongata separated. The cerebrum was then divided by a section along the median line, separating it as nearly as possible into two equal halves.

*Removal of dura.* The falx showed an interesting development, its frontal portion, especially in the region of the olfactory bulbs, being of considerable depth, then becoming very shallow along the middle of the length of the cerebrum and becoming very deep again in the intercerebral cleft in the caudal region of the cerebrum. A distinct longitudinal venous sinus as in the human brain is not present; but in place of it is a vein of some size lying to the right of the (intercerebral) cleft and receiving the contents of the dorsal cerebral veins. In connection with the weak development of the falx along the middle of its length, there was noticed an interdigitation of the gyres of the mesal surface of the hemispheres in this region. This intimate overlapping of the gyres on the mesal surfaces of the two hemispheres is possibly correlated with the deficiency of growth of the falx here and may serve, in a measure, to increase the firmness of the union of this region and prevent any undue strain upon the callosum which lies some little distance from the dorsal surface of the cerebrum.

This interdigitation of the mesal gyres is also present in the sheep where the falx is also deficiently developed. If the hemispheres be divided with a sharp knife without first separating the pial adhesion of the gyres, the gyres will be cut. An artifact of this nature has, indeed, been mistaken by one writer in an article on *Phoca*, for the cut surface of a bundle of fibers dorsal to and larger than the callosum and designated by him as the commissura suprema.

The tentorium in *Callorhinus* is very strongly developed, apparently extending the whole depth of the transverse arch-like cleft between the cerebrum and cerebellum. The tough fibrous tissue of the tentorium is, moreover, very noticeably reinforced by the presence of osseous tissue. Where the falx



joins the tentorium there is an extension of this osseous tissue in a vertical direction into the falx, a circumstance which certainly is not common in the majority of other animals but has been noted by Turner in *Macrorhinus*.

*Terminology.* With the existing uncertainties relating to the homology of the fissures of the brains of the carnivora and that of the human species, much confusion has resulted in the present nomenclature. Some have made a direct homology, others have proposed a fissural type solely and only for the lower forms, while still others have blended the two and some have utilized a system of names devised by themselves. On the lateral surface of the various fissured brain types there is at least one fissure—the Sylvian—which is quite constantly present, and on the mesal surface, the hippocampal fissure.

In the matter of nomenclature no attempt has been made to follow the law of priority, but those fissural names, whether of old or recent date which seemed most appropriate concerning position and relation, have been adopted, and, with perhaps but one or two exceptions, no new names have been introduced. It has been the purpose to use an intrinsic terminology and to substitute for the sometimes indefinite terms, anterior, posterior, superior and inferior, terms of more universal applicability, cephalic, caudal, dorsal and ventral. For cephalic and caudal Professor Wilder has recently suggested praeal and postal as equivalents, and for cephalad and caudad, praead and postad.

Where certain of the fissures or gyres have been submerged for a portion or the whole of their course, they have been designated as such, or the equivalent terms, subfissure or subgyre proposed by Wilder, have been used.

In the study of fissures mere surface appearances are not accepted as final. A fissural entity is not always easy to define. The best apparent guide is the relative depth throughout the course of the fissure. We may commonly assume that the greatest depth is at about the middle of its length and that it becomes gradually shallow toward each end until it reaches the surface. Such a simple condition, however, does not usually exist. One fissure may join the end of another, giving the ap-

pearance at the surface of a long continuous fissure. By separating its walls or "sounding" its depth the true state of affairs is easily perceived. The presence of a shallow whether it be near or at a distance from the end of a fissure would seem to indicate that at some time during development this shallow has been or will be represented at the surface and separate two independent fissures.

#### CALLORHINUS URSINUS.

*Cranial Nerves.* The cranial nerve roots of *Callorhinus* are well developed and need no special comment. In the case of the optic nerves we do not find the X-shaped chiasma as in *Phoca*, but the nerves run parallel to each other for a short distance from the chiasma before diverging toward the eyes.

The third pair or oculomotor nerves have a straight lateral direction from their apparent origins, but at the lateral border of the hypophysis they bend abruptly upon themselves and proceed cephalad forming a very distinct right angle.

The olfactory lobes are fairly well developed.

*Fissures.* No special mention will be made of the gyres (convolutions). These are naturally formed by the fissural depressions and it is believed that a careful description of these furrows will by implication include that of the gyres sufficiently for our present purpose.

The olfactory fissure is completely hidden by the olfactory crus and bulb; when these are removed a shallow fissure is apparent which becomes deeper toward the base of the lobe.

Forming the lateral boundry of the olfactory lobe is the rhinal fissure which passes in a caudo-lateral direction to the Sylvian. An apparent continuation of the rhinal from the Sylvian is known as the post-rhinal fissure. It extends in a meso-caudal direction for a centimeter and a half, stopping just short of the cleft between the cerebrum and the cerebellum. A careful examination of the postrhinal shows that it has no connection whatever with the rhinal but is continuous, superficially at least, with a subfissure (postica?) lying in the caudal wall of the Sylvian.

*Lateral Aspect.* The Sylvian is a convenient fissure to begin with. There is usually some evidence of it if the brain is at all fissured, and in the lower animals, at least, it forms a center around which other fissures are more or less regularly arranged. In *Callorhinus* the Sylvian extends in a dorso-caudal direction, inclining somewhat toward the vertical. Apparently it terminates in a fork, but when the walls of the fissure are divaricated it is seen that the cephalic or anterior branch is really another fissure, which, after its superficial union with the Sylvian, becomes a submerged fissure lying just beneath the surface of its cephalic wall and running parallel with it to the base of the brain, but not actually connecting either with the Sylvian or with the rhinal. The Sylvian on account of the subfissural complication appears to be a larger fissure than it really is.

In a former paper<sup>1</sup> attention was called to the fact that this vertical fissure (superficial vertical branch of the Sylvian) had been mistaken for the true Sylvian. Both fissures are well marked and cannot be ignored, but it is an unusual circumstance for the Sylvian to assume a strictly vertical position in the adult and there would, moreover, remain a fissure in the usual situation of the Sylvian unaccounted for. In my former paper I designated this vertical fissure as the Anterior of the Felidae, and found at a later date, while consulting Krueg's article<sup>2</sup> that he questioningly represents a similar fissure by the same name in *Calocephalus* (*Phoca*) *vitulinus*. *Callorhinus*, while showing this fissure similarly situated, instead of elucidating the complications, seems rather to add to them and to suggest a probable doubt as to the correctness of the homology with the anterior fissure. Indeed, the conditions are strongly suggestive of its being nothing more than the detached frontal portion of the super-sylvian fissure. An examination of the brains of certain bears tends to illuminate this view. In the family *Ursidae* as

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<sup>1</sup>'96. P. A. Fish. A note on the Cerebral Fissuration of the Seal (*Phoca Vitulina*). Jour. Comp. Neurol. VI, 15-19.

<sup>2</sup>'80. J. Krueg. Ueber die Furchen auf der Grosshirnrinde der zonoplacentalen Säugethiere. Zeit. f. wiss. Zoologie, XXXIII, 595-672, 5 plates.



in the *Canidae* the super-sylvian forms a complete arch, the caudal portion being known as the posterior supersylvian (Krueg), or postsylvian (Owen). The frontal portion of this arch varies in its distance from the Sylvian. Occasionally the frontal and caudal portions are about equally distant, but when there is any difference in this distance, it appears that the frontal portion approaches more closely to the Sylvian than does the caudal. In *Ursus arctos*, or the brown bear, Krueg figures the frontal portion of the supersylvian as approximating very closely to the Sylvian. The condition in *Callorhinus* might be considered as a stage just beyond this. In the brown bear the frontal portion of the supersylvian is still visible upon the lateral surface close to the Sylvian. In the case of the seal it has passed over the brink, so to speak, and is no longer visible its entire length on the lateral surface. The following diagrams will illustrate the conditions more clearly.

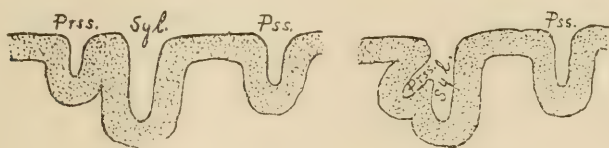


Fig. 1.

Fig. 2.

*Figs. 1 and 2.* A diagrammatic representation of the relation of the Sylvian and supersylvian fissures in the bear and seal, as if seen in section. *prss*, pre-supersylvian. *pss*, post-supersylvian. *Syl*, Sylvian fissure.

At the bottom of the Sylvian fissure lies the insula, presenting but a slight degree of development. There is a suggestion of a circuminsular fissure but in other respects the surface is entirely smooth. In the caudal wall of the Sylvian is a well marked subfissure. It separates a portion of the concealed cortex, forming a subgyre, which from its size and position might be easily mistaken for the insula. The appearances would suggest that the subfissure is the postica and the subgyre a remnant of the Sylvian gyre.

The supersylvian fissure shows some variation on the two sides. It presents the usual arrangement on the right hemisphere, forming, superficially at least, a complete arch around

the Sylvian. The presence of a shallow and a slight bifurcation near the level of the free end of the Sylvian indicates the separation of a postsupersylvian fissure, postsylvian of other writers. Plate I, Fig. 4. The supersylvian curves around the free end of the Sylvian at a rather sharp angle and soon apparently enters the Sylvian, but in reality is submerged in its cephalic wall. A very short cephalic branch is given off toward the ansate fissure before the supersylvian enters the Sylvian. On the left hemiserebrum there are three distinct portions; the postsupersylvian has a slightly more oblique dorso-caudal course, the supersylvian proper is quite branching and more inclined to a vertical than a horizontal course. One of its branches appears to enter the Sylvian from behind but a shallow shuts off any deep connection. The frontal portion appears as a surface fissure for only one third of its course, then, as on the other side, it becomes submerged in the Sylvian. As this portion bears much the same relation to the supersylvian as the postsupersylvian whether they be disconnected or not, the frontal portion will be designated as the presupersylvian fissure. In the second specimen of the brain of an adult *Callorhinus*, kindly loaned to me by Mr. True, the executive curator of the U. S. National Museum, both hemiserebrums showed a distinct separation of the postsupersylvian, more pronounced than on the right hemiserebrum of the pup; but there was no separation nor distinct appearance of a shallow indicating an independent presupersylvian as in the left hemiserebrum of the pup. In the adult, as in the pup, each supersylvian gave off a short cephalic branch before entering the Sylvian.

The Lateral fissure, on account of the breadth of the brain, does not show in its entirety upon the lateral aspect. It is twelve centimeters long, by far the longest fissure, and is seen for a short portion of its course upon the ventral aspect extending, on the left hemiserebrum, to within five millimeters of the ventral portion of the postsupersylvian. It lies in this region just in advance of the margin of the cleft between the cerebrum and the cerebellum. It then arches caudo-dorsally approximately parallel with the hemiserebral margin but receding from

it until it fully reaches the dorsal surface, then approaching to within eight or nine millimeters of the intercerebral cleft, it continues its arched course in a cephalo-ventral direction approaching to within five millimeters of the presupersylvian fissure at about the level where the latter becomes submerged in the Sylvian.

The lateral is a deep fissure and no distinct evidence of shallows could be detected along its course although in certain places the presence of submerged buttresses interfered to some extent with the soundings, the average depth being from ten to thirteen millimeters. The cephalic extremity of the fissure terminates in a fork, more marked on the left hemisphere than on the right. Does this widely forked termination represent the ansate fissure? It has the same appearance and relation to the lateral as seen in the cat, and provisionally, it is here so designated.

The gyre, bounded by the lateral and supersylvian fissures and its parts, is indented by numerous branches originating from the above named fissures. There are also occasionally independent minor fissures present in this gyre.

The Ectolateral fissure. The ectolateral on the right hemisphere is a distinct fissure. It begins on the ventral surface near the termination of the postrhinal; it then proceeds dorso-caudally, parallel with the postsupersylvian and for about the same distance. On the left side it is a shorter fissure and superficially is continuous with the dorsal portion of the postsupersylvian but a shallow separates a deeper connection. On the left side of the adult *Callorhinus*, a somewhat similar condition exists except that the superficial union of the ectolateral is with the ventral portion of the postsupersylvian.

The Coronal fissure is about three centimeters in length and extends except for a slight caudal convexity in an almost vertical (dorso-caudal) direction. Its greatest depth is eight millimeters. On the right hemisphere it gives off a slight spur pointing toward the Sylvian. In *Callorhinus* it represents, perhaps, the least complicated fissure in the brain.

The Cruciate fissure is not at all represented upon the me-



sal surface of the brain. It is seen best from a dorsal view. It arises at the margin of the intercerebral cleft. It arches in an obliquely cephalo-lateral direction. From the cephalic extremity of the cruciate at a depth of fifteen millimeters there passes off another fissure, which Krueg has represented as the precruciate in certain carnivora, nearly to the mesal margin just dorsal to the olfactory bulb. The depth of these fissures at their junction is from 12-15 millimeters. Between these fissures and the intercerebral cleft there is a triangular shaped area to which Mivart has applied the name of "ursine lozenge" (Turner), thought by Mivart to be of considerable significance. Just caudal to the cruciate fissure is a small fissure corresponding to the postcruciate of Krueg. On the left hemicerebrum it is tri-radiate, on the right it is straight.

The Supraorbital fissure has no connection with the rhinal. Its length is 25 millimeters and its depth 8-10 millimeters. It has a slight lateral convexity but has no branches.

The Medilateral fissure. The name of this fissure is particularly appropriate in *Callorhinus*; not only is it on the mesal side of the lateral fissure, but for a portion of its course is actually on the mesal aspect of the brain. It curves around the caudal margin of the hemicerebrum just on the verge of the cerebro-cerebellar cleft. Between the lateral and medilateral fissures there is a gyre averaging about 15 millimeters in width in which there are two or three secondary fissures, which would seem to indicate an attempt at the division of this gyre into two.

*Mesal Aspect.* The callosal fissure presents no marked peculiarity except upon the left hemicerebrum where, instead of continuing around the genu of the callosum, it proceeds toward the dorsal margin, or is continuous with a fissure coming from this margin. On neither hemicerebrum is there any appearance of a fissure immediately surrounding the genu. The hippocampal fissure occupies its usual position, arching from the splenium around the optic thalamus to the tip of the pyriform or temporal lobe.

The Splenial fissure. On the right hemicerebrum, this fissure, if prolonged on the dorsal aspect, would be continuous

with the cruciate. It is separated by a gyre 4 millimeters in width. The fissure passes ventro-caudally and a little beyond the splenium on the ventral aspect and it apparently terminates in a wide fork, or else enters a fissure passing at right angles to its own course. Sounding the fissure at this point gives some indication of a shallow separating the caudal branch of the fork. Following the appearance designated by Krueg in his diagrams of the conditions found in some of the carnivora, the splenial proper includes the ventral branch of the fork, while the dorsal branch may represent what he calls the postsplenial. On the left hemiserebrum the splenial fissure penetrates the hemiserebral margin and appears for a short distance on the dorsal surface. A smaller but well defined fissure lies in front of the splenial. On the left side it cuts the dorsal margin. For the present we may designate it as the presplenial fissure. It corresponds very well with the fissure which Kükenthal has called *fissura sublimica anterior*.

The Marginal or supersplenial just passes the meso-ventral margin of the hemiserebrum about ten millimeters caudad of the splenial. It extends approximately parallel with it to the dorsal margin which it cuts and on the right hemiserebrum extends on the dorsal surface for about 15 millimeters. On the left hemiserebrum the fissure branches just at the margin. The main portion however continues obliquely latero-cephalad for about 20 millimeters. In the gyre between the splenial and supersplenial fissures a well represented secondary fissure is seen.

A well defined but unnamed fissure lies on the meso-ventral surface. It arises at the caudal margin and proceeds in an angular course toward the ventral end of the splenial, it then swerves cephalo-laterad and terminates not far from the post-rhinal. Its position corresponds approximately to the collateral fissure in the human brain. This tentorial surface of the cerebrum has numerous secondary fissures and branchings some of which seem large enough to merit special mention. One such fissure lying parallel with the postsplenial suggests a similarity to the occipital. It cuts the hemiserebral margin slightly and the relation of the lateral fissure at this point suggests in a way

the paroccipital of man. This occurs on the left hemisphere. On the right the postsplenial has much the same appearance.

At the cephalic end of the mesal surface beyond the genu of the callosum, there are two pretty well marked fissures. The one nearest the callosum corresponds to the genualis of Krueg, part of falcial—Owen, or falcial—Wilder. On each hemisphere this fissure cuts the dorsal margin slightly. The other and more slightly developed fissure lies nearer to the olfactory bulb. It does not reach the dorsal margin but extends farther in the ventral direction. This fissure corresponds to the rostralis of Krueg, part of falcial—Owen, subfalcial—Wilder.

#### PHOCA VITULINA.

The frontal portion of the cerebrum is more foreshortened than in *Callorhinus* and there is therefore a slightly different arrangement of corresponding fissures in that region. One of the most striking differences is the olfactory portion of the brain. In *Callorhinus* it is the larger, the olfactory bulb is of considerable size, the crus is correspondingly wide and lies flush with the mesal surface. In *Phoca* the bulb is relatively smaller and the crus has atrophied to scarcely more than a pedicle, it lies deeply imbedded in the olfactory fissure and it is removed 6-8 millimeters from the mesal surface by a portion of the cortex which projects fully 5 millimeters beyond the crus.

The precribrum (anterior perforated space) is well developed and shows with greater distinctness than in *Callorhinus*. The rhinal fissure is apparently continuous with the Sylvian, but upon raising the overlapping portion of the frontal lobe, it is seen to maintain its continuity and to appear again caudal to the Sylvian as the postrhinal, differentiating a larger pyriform lobe than in the case of *Callorhinus*. There is no connection between the postrhinal and the subfissure in the caudal wall of the Sylvian as in *Callorhinus*.

*Lateral Aspect.* The Sylvian fissure pursues a much more obliquely dorso-caudal course than in *Callorhinus* and presents the same amount of complexity with relation to the surrounding fissures. In its caudal wall lies a subfissure (postica ?) and

the intervening Sylvian gyre. Both are relatively better developed than in *Callorhinus*. The supersylvian has much the same relation to the Sylvian as in *Callorhinus*. It is not distinctly separated from the postsupersylvian although the interlocking of some of the subgyral buttresses suggests the possibility of an attempt at separation. On each hemiserebrum there is a continuation of the postsupersylvian dorso-caudad beyond the supersylvian.



Fig. 3.



Fig. 4.

*Fig. 3.* Cross section of a fissure, showing the obliquity of the walls.

*Fig. 4.* A diagram to show the difference in the course of a fissure at its surface and depth. The heavy lines represent the fissure walls at the surface. The dotted lines and arrows represent the buttresses (b) formed by the bulging of the deeper portion of the wall of the fissure.

The frontal end of the supersylvian apparently forks, one branch bending toward the Sylvian, the other continuing cephalad. The ventral branch has a superficial union with the vertical fissure which has been mistaken for the Sylvian. In my former paper (l. c.) I designated this fissure as the anterior. Krueg also had taken the same view. From the conditions already described in *Callorhinus*, it seems to me that this fissure is after all a disconnected portion of the supersylvian and that presupersylvian would in some ways be a suitable name for it. It is submerged in the cephalic wall of the Sylvian for the ventral third of its course. In *Callorhinus* the ventral two-thirds of the corresponding fissure becomes submerged.

The lateral fissure, as in the case of *Callorhinus*, is the longest fissure in the brain. In *Phoca*, however, it is confined entirely to the dorsal aspect of the cerebrum, and at its caudal end it appears to terminate in a widely diverging fork or perhaps a small transverse fissure, possibly corresponding to the lunate (Wilder) of the cat. Its course is approximately parallel with the intercerebral cleft and is somewhat tortuous. At



its cephalic end it appears to communicate with the cephalic branch of the supersylvian. This appearance will be discussed more fully under the description of the ansate fissure.

The ectolateral fissure occupies a relatively higher or more dorsal and caudal position than in *Callorhinus*. It is of a more secondary character and courses approximately parallel with the postsupersylvian.

The cruciate, unlike that of *Callorhinus*, is represented upon both the mesal and dorsal aspects. On the left hemiserebrum a shallow is present in the dorsal portion not far from the margin. No distinct "ursine lozenge" is present here as in *Callorhinus*. The foreshortened condition of this region may have something to do with its absence.

A well defined postcruciate fissure is present on the left side. It presents a zygial (Wilder) or quadriradiate form. A slight secondary fissure near the olfactory bulb may represent a rudimentary precruciate fissure.

The superorbital fissure shows a better development than in *Callorhinus* and similarly has no connection with the rhinal. But the opposite end, dissimilarly, extends farther and is overlapped by the olfactory bulb.

The medilateral is not present in *Phoca* as a distinct fissure. Its location is occupied by a series of short disconnected fissures.

The coronal fissure is a relatively longer fissure than in *Callorhinus* but is not so entirely disconnected from adjacent fissures. Its dorsal end lies caudal to the cruciate. On the left hemiserebrum it is separated by a shallow from an apparent connection with a continuation of the cephalic branch of the supersylvian. On the right hemiserebrum the shallow is suggested by the interlocking at this point of two submerged buttresses.

The ansate fissure, while not distinctly represented as an independent fissure, would, it seems to me, be indicated by the fissure extending from the coronal to the cephalic branch of the supersylvian, where, on each hemiserebrum, the interlocking of submerged buttresses would again suggest a shallow shutting it

off from the branch of the supersylvian, and then continuing to the lateral fissure where a slight spur pointing toward the inter-cerebral cleft might indicate its separation from the lateral. Owen in his figure of the hemicerebrum of *Phoca* represents a corresponding fissure as the coronal.

*Mesal Aspect.* There is a slight appearance of the callosal fissure in the splenial half of the callosum, but none at all for the remaining half.

The hippocampal fissure is well developed and needs no special comment.

The splenial fissure is well developed and in general is as described for *Callorhinus*, except that its position is farther removed from the frontal portion of the cerebrum and that its cephalic end cuts the margin and is shown upon the dorsal surface. The postsplenial has about the same relations as in *Callorhinus*.

The fissura sublimica of Kükenthal<sup>1</sup> is poorly represented in my specimen of *Phoca* and is somewhat confused with smaller branches and secondary fissures. It lies between the splenial and the callosum. Kükenthal finds this fissure also present in *Phoca groenlandica*, *Phoca barbata*, *Macrorhinus leoninus* and *Otaria jubata*. In *Callorhinus* there was no appearance of this fissure whatever. The fissura sublimica anterior of the same author is more clearly represented. In my former paper, on account of its position dorsal to the callosum, I designated it questioningly as the supercallosal. On the left hemicerebrum it is well developed and connects with the cruciate. On the right side, however, the fissure is independent and much smaller. In addition to this fissure, on each hemicerebrum, there is another dorsal to it and in front of the splenial. In *Callorhinus* I have called it the presplenial.

The marginal or supersplenial is well shown in *Phoca* as in *Callorhinus* but lies nearer to the dorso-caudal margin, approximately parallel with the splenial. In the intervening gyre there are a few secondary fissures.

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<sup>1</sup> Untersuchungen an Walthieren, 1889.

On the meso-ventral surface a fissure corresponding to the collateral is also present, but, unlike *Callorhinus*, it has connection with the postrhinal. Between the collateral and the post-splenic there is another well marked but unnamed fissure which is parallel to the former. It corresponds perhaps to the fissure in *Callorhinus* which I have spoken of tentatively in connection with the occipital.

The genualis and rostralis are represented but the latter differs from that in *Callorhinus* in being much less developed and occupying a more ventral position at a more or less acute angle to the genualis.

#### URSUS AMERICANUS.

This brain, while fairly well preserved, had been considerably mutilated in removal, so that for purposes of illustration and reference, a specimen from *Ursus thibetianus*, kindly loaned by Prof. B. G. Wilder,<sup>1</sup> was utilized; so that while the figures of the lateral and mesal aspects are from the latter specimen, the description is based almost entirely upon the former. The general arrangement of the fissures is similar and the minor details need not cause misapprehension. The fissural plan of the brain is much like that of the canine, minus the first circum-sylvian arch.

The olfactory bulbs and crura are far superior in size to those of either of the seals. The olfactory fissure is likewise well marked.

The rhinal fissure passes into the Sylvian and continues, after forming an angle delimiting a well developed pyriform lobe, as the postrhinal and ending freely. The subfissure (postica?) in the caudal wall of the Sylvian extends to and, on one side, actually appeared to communicate with the postrhinal.

*Lateral aspect.* The Sylvian is directed in the usual dorso-caudal direction at the bottom of which is a small and simple area representing the insula. There is no appearance of a trans-

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<sup>1</sup> Papers, chiefly anatomical, presented at the Portland Meeting of the A. A. S., August, 1873, are devoted largely to a description of the brains of Carnivora.

insular fissure although the presence of a subgyre and subfissure (postica?) in the caudal wall of the Sylvian might superficially indicate it.

The supersylvian fissure forms a complete arch around the Sylvian. There is no indication of a separation of a postsupersylvian except near the free end of the Sylvian where a branch from the supersylvian extends into the adjacent gyre.

The lateral fissure forms a curve approximately parallel with the supersylvian. As compared with *Phoca* and *Callorhinus* it is much shorter. If the conception of the ectolateral is correct, the latter is continuous caudally with the lateral, a slight spur indicating the place of probable separation. The ectolateral extends parallel with the postsupersylvian but its ventral end does not reach so far in *Ursus americanus*, while in the Thibet bear the reverse is the case.

The ansate fissure is a cephalo-ventral continuation of the lateral, a small spur of the latter indicating a point of separation. The ansate describes a curve, the convexity pointing toward the Sylvian.

The coronal fissure continues from the ansate and ends freely near the superorbital. The convexity of its curve like that of the ansate points toward the Sylvian. The point of its separation from the ansate is indicated by a spur more marked than that between the ansate and the lateral.

The superorbital, unlike *Phoca* and *Callorhinus*, has a very distinct connection with the rhinal fissure at about half of the distance from the Sylvian fissure to the olfactory bulb. It curves cephalo-dorsad with its convexity pointing cephalad.

The cruciate fissure is more highly developed than in either of the seals. It appears slightly upon the mesal aspect and extends obliquely cephalo-laterad on the dorsal surface. Around its free end the coronal fissure demarcates a well-formed sigmoid gyre. The appearances found in *Phoca* approximate the conditions regarding the gyre more than in *Callorhinus*.

Between the cruciate and ansate lies the postcruciate fissure. On the left hemicerebrum it is well marked, on the right it is smaller and superficially connected with a minor fissure,



On the right hemisphere a branch is given off from the cruciate extending cephalo-mesad. It is the precruciate fissure. On the left hemisphere it is an independent fissure. In neither case does it reach the mesal surface. The precruciate with the cruciate forms a well-defined triangular area—the “ur-sine lozenge” of Mivart. On the dorsal surface between the lateral fissure and the intercerebral cleft there is a well marked fissure but it is not as deep as the other fissures. It is the con-finis. On the right hemisphere a short fissure connects it with the lateral.

The medilateral fissure arises at the caudal end of the cerebrum near the mesal margin, in much the same position as in *Callorhinus* and continues down the ventral aspect close to the caudal margin.

*Mesal Aspect.* The splenial fissure does not reach the dorsal margin as in the case of *Phoca* and as on one side in *Callorhinus*. Its cephalic end is, also, nearer the caudal end of the cerebrum than in either of the other two forms. In this respect the fissure occupies an intermediate position in the *Phoca*. It arches around the splenium of the callosum and courses along the tentorial surface of the cerebrum as far as the caudo-lateral margin, ending eight millimeters from the free end of the post-supersylvian. Two or three short branches are given off along its course. Beyond the presence of a slight spur there is no evidence of a postsplenial fissure, nor of a supersplenial or marginal as in the case of the seals. A well developed presplenial or fissura sublimica of Kükenthal is present, resembling that of *Phoca* more than *Callorhinus*. No distinct fissura sublimica was present except in the case of the Thibet bear where a small minor fissure held the proper position.

The genual and rostral fissures were present and occupied the same general relation to the cephalic end of the callosum as in *Callorhinus*. The callosal and hippocampal fissures have the same general relations as in other forms.

## ZALOPHUS CALIFORNIANUS.

Through the kind permission of Professor Wilder I was permitted to remove the brain from this young sea lion. Its mother came originally from the Pacific coast and the present specimen was found dead in the cage with her while in transit to the East and was presumably not far from "term." It measured 43 centimeters long and has been in the Cornell museum of Vertebrate Zoology for some years.

The brain was in a fairly good state of preservation and was photographed soon after its removal. It was too delicate to permit of much manipulation and some of the fissures were not sounded as thoroughly as in the other specimens. The cerebrum of this specimen does not show the same degree of complexity relative to the fissuration as indicated by Murie<sup>1</sup> in *Otaria jubata*. A direct comparison of the fissures, however, is not easy as the latter author attempts to homologize them with those of the human cerebrum.

The olfactory apparatus is well developed. Not as largely as in the bear, however, but greater than either of the seals. The rhinal fissure, as in the other forms, is well marked and passes caudad into the mouth of the Sylvian fissure. The postrhinal is formed from the subfissure (postica ?) and has no connection whatever with either the rhinal or Sylvian.

*Lateral Aspect.* The Sylvian is prominent and occupies its usual position. In its caudal wall is a subfissure (postica ?) and subgyre which as in *Callorhinus* is continuous on the ventral aspect with the pyriform or temporal lobe.

The supersylvian with its cephalic and caudal portions, the pre- and postsupersylvian, is more nearly in accord with the condition found in the bear than in either of the seals. It represents an intermediate condition between the two. The pre-supersylvian lies very close to the Sylvian but does not actually enter it as in the seals. Its average distance from it is about 4 millimeters; while the distance from the Sylvian to the post-

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<sup>1</sup> 1874. Transactions of the Zoological Society of London.

supersylvian is four times as great or 16 millimeters. There is no sign of disconnection between either the supersylvian and the postsupersylvian, or the supersylvian and the presupersylvian. The supersylvian forks or sends out a branch cephalad connecting with the ansate fissure exactly as in *Phoca*.

The lateral fissure is relatively to the length of the cerebrum shorter than in any other forms. Its cephalic end and its relation to the ansate is again exactly the same as in *Phoca*. On the left hemiserebrum the lateral is disconnected at a little more than half of its length, by a narrow isthmus.

The coronal fissure corresponds with that of *Phoca*, connecting, superficially at least, with the ansate and thus indirectly with the cephalic branch of the supersylvian and the lateral.

The ansate fissure, as has already been intimated, like that of *Phoca* is irregular in its form and connects with the fissures above mentioned.

The ectolateral fissure is quite well down toward the ventral portion of the cerebrum and as in *Callorhinus* appears upon the ventral aspect.

The medilateral fissure is scarcely perceptible on the lateral aspect; it lies exactly along the caudal margin of the hemiserebrum as in *Callorhinus* and is better seen in a mesal view.

The cruciate accords, in position and relation, more closely with the conditions found in the bear and *Callorhinus*; but while it reaches to the mesal surface of the hemiserebrum it does not cut it as far as in the bear and *Phoca*.

The precruciate and the postcruciate fissures are likewise present and have exactly the same relations as in the bear and *Callorhinus*.

*Mesal Aspect.* The callosal fissure is well developed. On the right hemiserebrum it does not continue around the genu as in the left.

The splenial fissure does not extend as far cephalad as in *Callorhinus*, nor as far dorsad as in *Phoca*. It is situated more closely to the splenial half of the callosum than in either of the preceding or in the bear. A branch is given off in the region of the splenium proper which seems comparable to the

postsplenial in the seals. A slight spur in this region in the bear may indicate an analogy.

The presplenial is not represented as a distinct fissure on the left hemiserebrum, the only possible suggestion of it being a forking at the cephalic end of the splenial. On the right hemiserebrum a small but distinct fissure lying cephalad of the splenial may represent the presplenial.

The marginal fissure is well represented and on both hemiserebrums cuts the dorsal surface as in *Callorhinus*. In *Phoca* although relatively long it does not reach the dorsal margin at all. In the bear the marginal fissure is not represented.

The genual and rostral fissures are but slightly developed in this specimen and bear the same relations as in other forms.

The cruciate fissure shows slightly on the mesal aspect and in its relations to the other parts resembles that of the bear more than any of the others.

#### FISSURAL INTERPRETATIONS OF OTHER WRITERS.

The Sylvian fissure, in *Phoca* at least, has been located as a vertical fissure (presupersylvian) which has, for a portion, only, of its length, been submerged in the cephalic wall of the true Sylvian. Numerous writers have also described this condition as the anterior and posterior branches of the Sylvian. The two fissures morphologically are entirely distinct. In *Hyrax* Krueg does not represent any indication of a Sylvian fissure whatever.

The supersylvian is very commonly called the suprasylvian. Leuret et Gratiolet have confused this fissure with the lateral in *Phoca*.

Following Krueg the fissure which is designated as the post-supersylvian, is commonly known as the postsylvian of Owen. What I have designated as the presupersylvian and which is only exceptionally independent, is usually described as the anterior or frontal portion of the supersylvian.

A fissure corresponding to the coronal is represented by Krueg as the presylvian in *Phoca*. Kükenthal makes a similar representation. Turner in *Macrorhinus* represents a corresponding fissure as the presylvian and a branch connecting with it



as the coronal. In *Trichecus* (walrus) he figures as the presylvian an apparent continuation of the lateral, and represents as the coronal an apparent continuation of a third arched fissure designated by him as the medilateral.

The superorbital fissure in carnivora generally is designated as the presylvian by many writers.

The cruciate fissure is shown by Krueg, in *Phoca*, as existing only on the mesal aspect, occupying the position of the presplenial, or anterior sublimica of Kükenthal. Leuret et Gratiolet represent the fissure as seen on the ventral aspect at the cephalic end. Other writers place it as usually seen in carnivora at the cephalic end of the dorsal aspect where it may or may not reach the mesal surface.

#### THE LATERAL VENTRICLE (PARACOELE.)

On removing the dorsal portion of the hemicerebrum just dorsal to the callosum the lateral ventricle is revealed. In the bear the cavity bends cephalo-ventrad to form the precornu and caudo-latero-ventrad to form the medicornu. The striatum is a well defined body forming a portion of the floor of the ventricle in the cephalic region. Parallel with the oblique margin of the striatum is the fimbrial margin of the hippocamp. Between these two margins—the rima (great transverse fissure) the choroid (para) plexus—a continuation of the velum enters the floor of the cavity. The hippocamp pursues its usual curved direction in the medicornu.

In *Phoca* the lateral ventricle is relatively very much larger than in the bear and the parts present quite different relations to each other. The striatum is the same as in the bear; along its margin is a well developed plexus, but between this and the fimbrial edge of the hippocamp there is an area equally as large as the striatum; this is the optic thalamus, but that portion of it represented in the floor of the cavity presents the same general appearance as to its surface (endymal) as do the other parts. The supposed delicate endymal membrane extending from the plexus to the fimbria has been designated as the paratela by Wilder. The hippocamp, then, is removed some little

distance from the striatum and arches around the surface of the thalamus in a ventral direction. Caudal to the hippocamp, the cavity is about as largely represented, and in size forms a disproportionately large postcornu. Along the mesal wall just caudal to the hippocamp is an ental ridge correlated with an ectal depression—the splenial fissure. This is comparable to the calcar or hippocampus minor of the anthropoid and human brains. It is larger in proportion than either of the above. The splenial in this case for a part of its course at least is, therefore, a total (Wilder) or complete (Cunningham) fissure since the whole thickness of the parietes is involved; the ental elevation being correlated with the fissural depression. In this specimen of *Phoca*, then, we have two total fissures, the hippocampal (always) and a portion of the splenial.

The conditions just described might naturally suggest a homology with the ape and human calcar and that the splenial fissure, in this seal possessing a postcornu, might be homologized with the occipital or calcarine fissure in man. A question might properly arise here as to which fissure it might be homologized with. In the human foetus the occipital is a total fissure, but loses its totality (ental elevation) in the adult. Its position might favor its homology with the splenial, for if the latter were rotated farther caudad it would come to occupy approximately the same position as the occipital. To homologize with the calcarine we would have to imagine a still farther rotation of the splenial. The calcarine is a total fissure throughout life and is the correlative of the calcar. Some doubt may therefore be expressed, assuming the homology to be reasonable, whether this hippocampus minor represents the occipital eminence—a foetal condition in the human brain, or the calcar—a structure persistent in the adult.

The relative disproportion in the growth of the caudal or occipital portion of the cerebrum may have some bearing in accounting for the presence of the postcornu. Tiedemann in his figure of the lateral ventricle of *Phoca* gives no indication whatever of a postcornu.

In *Callorhinus* the conditions resemble more closely those

in the bear; the rima is narrow and the thalamus does not appear at all in the floor of the ventricle. A slight caudal spur of the cavity at the medicornu represents the postcornu. The splenial fissure, so to speak, just escapes the cavity, lying immediately caudal to it.

In the walrus Turner<sup>1</sup> represents a dissection of this cavity but shows no indication of a postcornu, but in the text he states: "where the cavity of the ventricle curved downward and outward into the horn, an indication of a recess was seen in its posterior horn, but it did not amount to a cornu and there was no elevation which could be called a hippocampus minor."

Murie,<sup>2</sup> on the form and structure of the Manatee, figures a well developed postcornu. He states that, "there is an undoubted posterior cornu, a fully developed hippocampus minor and an eminence I am inclined to recognize as eminentia collateralis." The same author, On the Anatomy of the Sea Lion, *Otaria jubata*, figures a more extensive postcornu than is represented in the manatee and describes it as "stretching backwards and outwards with a very regular sweeping arch, and goes well back into the occipital lobe, terminating in a shallow tapering extremity. The eminentia collateralis is not distinctly defined; but what appears to represent the outwardly bulging hippocampus minor has a length of 0.7 of an inch, and at widest is 0.3 to 0.4 broad."

Wilder in the Anatomical Technology, in indicating the lines of inquiry likely to be most productive of results in the homology of the human and feline fissures, states that "between the ordinary carnivora and the monkeys are two groups whose brains should be studied with especial care; the seals have a rudimentary postcornu and occipital lobe, and these parts are said to be developed in the *Lemurs* which have affinities with both the carnivora and the primates."

In none of the accounts have I seen any direct mention of

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<sup>1</sup> '84. Turner, Report on the Seals collected during the Voyage of H. M. S. Challenger in the years 1873-1876.

<sup>2</sup> 1874. Transactions of the Zoological Society of London.

the correlation of the splenial fissure with the calcar in these aquatic forms. This fact, even if it be of no direct use for homology, is, at least, interesting.

## MONACHUS TROPICALIS.

In August, 1897, I was fortunate to obtain through the courtesy of Dr. A. H. Hassall, Washington, D. C., two brains, from male and female specimens of the West Indian Seal *Monachus tropicalis*. They arrived at an exceedingly opportune time for comparison with the other brains dealt with in this article. A study of their form and fissural relations throw much light on some of the points which seemed quite aberrant in *Phoca* when compared with *Callorhinus* alone.

The general form of the brain would suggest a position intermediate between the fur seal and *Phoca* particularly in the frontal region which is somewhat foreshortened and broader than in *Callorhinus*. The caudal portion of the cerebrum is much elongated, noticed particularly upon the mesal aspect when measured from the splenium of the callosum; as if, perhaps, to compensate for the foreshortened frontal region. The cerebrum also shows a slightly greater overlapping of the cerebellum. The olfactory bulb and crus resemble the corresponding parts in *Phoca*, but show a slightly greater development.

*Fissures.* Postica. In all four hemispheres, this fissure sends a branch to the surface, thus appearing superficially as a branch of the Sylvian. The postica is less easily distinguished in *Monachus* than in any of the other forms, as it is submerged practically to the bottom of the Sylvian fissure. In *Callorhinus* there is a branch corresponding to that of *Monachus* but it does not extend deeply enough to connect with the postica.

The postrhinal appears as the merest trace of a fissure and has a very superficial connection with the postica.

The Sylvian fissure. It is in the Sylvian region that we get numerous clues to the intermediate position of *Monachus*. In the brain of the female the Sylvian has practically the same direction as in *Callorhinus*. In the male, the true Sylvian really branches cephalad, although there is a superficial extension in



the usual dorso-caudal direction. Apparently some unusual conditions exist here, which may perhaps be accounted for by the nearly complete disappearance of the postica.

The presupersylvian resembles the corresponding fissure in *Phoca* regarding its extreme vertical position and apparent union with the Sylvian for only the ventral third of its course. It differs from *Phoca* in not being disconnected from the supersylvian.

The supersylvian fissure resembles that of *Phoca* in extending a branch of good size to connect with the ansate.

Postsupersylvian. In the two hemicerebrums of the male there was a connection between the supersylvian and the postsupersylvian much as in *Phoca*. In the hemicerebrums of the female there was an entire disconnection of these fissures.

The cruciate fissure more than in any of the others resembled that of *Phoca*. It forms a good intermediate stage between *Callorhinus* and *Phoca*. As with *Phoca* the fissure is represented on the mesal surface as much, if not more than upon the dorsal. In the left hemicerebrums of both brains the cruciate is apparently continuous with the splenial. Upon the right hemicerebrums there is no such connection.

Precruciate. In all four hemicerebrums the precruciate extends over upon the mesal surface for some little distance. It is more largely represented upon the dorsal surface and its lateral end makes a very decided curve toward the coronal fissure. There is almost a superficial connection between the cruciate and the precruciate. The conditions in *Phoca* indicate that such a connection has occurred even to the extent of their almost complete merge into each other.

"Ursine Lozenge." This area is, with the exception of *Phoca* where it is undistinguishable, smaller than in any other forms. It is nothing more than a narrow gyre, situated at a slightly lower level than the adjacent gyres, suggesting a probable preparation for the loss of its identity in *Phoca*.

Postcruciate. In *Monachus* this fissure was the least satisfactorily represented than in any of the other forms. In the two hemicerebrums, it does not seem to be represented at all,

unless we interpret a slight branch from the cruciate as representing it. In the right hemispheres the fissure is distinctly present but is very small.

The splenial accords more closely with *Phoca* in its position, reaching the mid-dorsal region instead of extending farther cephalad as in *Callorhinus*. It sends off a branch corresponding to the postsplenial as in other brains.

The presplenial is well represented in the two right hemispheres, but in the two left it appears to connect the true splenial with the cruciate. The interlocking of submerged buttresses at the proper points indicates a superficial connection merely.

The marginal fissure is more poorly developed than in any of the other forms except the bear. A series of short interrupted fissures takes its place.

A well marked collateral fissure is present and resembles the corresponding fissure in *Callorhinus* very closely.

Postcornu. Perhaps the most important point in connecting *Monachus* with *Phoca*, is a very well developed postcornu. *Callorhinus* shows the merest trace of one and in the bear it is absent. In *Monachus* it does not go so far as in *Phoca*, a great portion of the caudal wall being solid. The floor of the postcornu in *Monachus* is quite distinctly convex. This convexity of the internal surface is found to be correlated with an external depression, the lower or ventral portion of the splenial fissure. At the more vertical portion of the fissure, namely, opposite the caudal end of the callosum, the splenial fissure loses its totality and becomes an ordinary fissure for the remainder of its upward course. The postcornu stops at the level of the depth of the splenial fissure in the callosal region. We have not, therefore, as in *Phoca*, a well developed calcar (*hippocampus minor*). The internal convex surface already spoken of in connection with the ventral portion of the splenial fissure, offers a suggestion as to the inception of the calcar which finds its fulfillment in *Phoca*.

## GENERAL CONSIDERATIONS.

The average canine brain, as a matter of convenience, may be accepted as a simple type of a carnivore brain. The fissures are clearly demarcated and there is an absence of much branching or secondary fissuration.

Around the Sylvian there are three arched fissures separating the cortical substance into four distinct folds or gyres. In the brains of cats and occasionally in dogs we find that the arched fissure nearest the Sylvian is not a complete one; that only the pillars are represented, the keystone being absent.

In *Hyena* and *Proteles* the frontal portion of this arch is wanting (Krueg) but the caudal portion, *fissura postica*, is well represented. Correlative with this state of affairs the postsupersylvian, as compared with the presupersylvian, is situated at least twice as far from the Sylvian fissure.

In certain others of the carnivora no trace of the first arch or Sylvian gyre with its limiting fissure (*anterior-postica*) is at all present. The first arch with its fissure has disappeared, apparently swallowed up by the Sylvian. There are represented then on the lateral aspect only two arched fissures, the supersylvian and on the lateral aspect only the three gyres which they separate. In those forms in which only the two arched fissures are present, if the distance from the frontal portion of the supersylvian to the Sylvian be compared with the distance from the latter to the postsupersylvian, it will generally be found to be less in the former, and this becomes much more emphasized in the case of some of the bears, where the frontal portion of an undoubted supersylvian almost enters the Sylvian fissure.

In his description of the brain of the Polar bear, *Ursus maritimus*, Turner says: "On opening up the Sylvian fissure I found to my surprise that a definite arched convolution was completely concealed within it. It was separated from the convolution which bounded the Sylvian fissure by a deep fissure which was also concealed. Its anterior limb, not quite so bulky as the posterior, was continued into the supraorbital area immediately external to the rhinal fissure and to the outer root of the olfac-



tory peduncle. Its posterior limb reached the postrhinal fissure and the *lobus hippocampi*. I could not but think that we had here, more completely than either in the walrus or seals, a sinking into the Sylvian fissure of the convolution which ought to have bounded it, so that both the Sylvian convolution properly so called, and the suprasylvian fissure were concealed within it. If this be a proper explanation of the arrangement, then the three convolutions on the cranial aspect would be saggital, mediolateral, and suprasylvian; whilst the two complete curved fissures between them would be the mediolateral and lateral."

The question quite naturally arises if the fissure concealed in the Sylvian may not be the equivalent of the anterior-postica of Krueg and the two remaining visible on the cranial surface, the supersylvian and lateral.

The medilateral of other authors does not attain the size nor continued length in the frontal direction as ascribed to the mediolateral by Turner. And furthermore there is in some forms, as in the seals, a well defined medilateral in addition to the two principal fissures.

In a specimen of *Ursus americanus*, I had the good fortune to discover a stage one step beyond that described by Professor Turner. On opening the Sylvian fissure I found in its caudal wall a completely submerged fissure, with a remnant of the Sylvian gyre which might possibly be mistaken for the insula. A true insula, although small, is present. This submerged fissure I take to be the disappearing vestige of the ectosylvian (Owen) or anterior-postica (Krueg). A study of foetal bear brains with reference to the distinct appearance of the first circumsylvian arch (anterior-postica) would be most important in this condition.

It would seem then that the condition thus described in the polar bear and American bear would represent the method of disappearance, rather than the appearance, of the first circumsylvian arch and prepare us for the conditions that we find in the sea lion (*Zalophus*) and the seals (*Phoca* and *Callorhinus*).

In the sea lion the conditions regarding the frontal portion of the Sylvian gyre are intermediate between the bears and seals. The presupersylvian fissure approaches very closely to



the Sylvian fissure and the intervening portion of the Sylvian gyre, besides being narrower than in the bear, has also sunk slightly lower than the adjacent surface as if prophesying the conditions found in the seals.

In the seals there appears to be some evidence, if the interpretation as to the frontal portion of the supersylvian fissure be correct, that after breaking up into branches with perhaps some disconnection of its parts, it shows a tendency to follow the example of the anterior-postica fissure, because in *Phoca*, at least, the supersylvian bifurcates a little beyond the free end of the Sylvian, one branch forming a well defined arch around it, the other branch passing on in the frontal region. The branch, however, which forms the arch is not a long one but it extends to and superficially connects with a vertical fissure which for half its distance is submerged in the frontal wall of the Sylvian, and crops out again on the ventral aspect of the brain. This condition holds for both hemispheres of *Phoca*. *Callorhinus* throws a little light on this matter. In the right hemisphere the supersylvian is clearly continuous with the vertical fissure submerged in the frontal wall of the Sylvian but gives off a very short frontal branch. Superficially it is continuous with the post-supersylvian but a shallow at this point indicates a partial separation. The direct continuity in the depth of the supersylvian with the vertical fissure would seem to point to the fact that the latter, after all, was nothing more than the frontal portion of the supersylvian, namely the presupersylvian.

In the left hemisphere the parts are a little more complicated. The post-supersylvian is entirely separated, the supersylvian is entirely distinct from the frontal portion and is quite irregular and branching in its course, but mainly vertical in its direction.

Thus, taking the canine brain as exemplifying a simple fissural pattern and passing through the *Felidae* and *Ursidae* and sea lion to the seals where the fissures are more numerous and complicated by the presence of branches of considerable size, and more or less disconnection of some of the principal fissures, we may arrive at some understanding of the relationship and

changes effected in passing from simple to complex conditions.

In the general form of the brains that of the sea lion seemed to bear closer resemblance to that of the bear than either *Callorhinus* or *Phoca*—the latter the least of all. The elongated and narrow frontal portion of the brain as seen in the bear is represented in *Phoca* by a foreshortened and broadened region, less marked in *Callorhinus* and still less in *Zalophus*.

The development of the olfactory lobes is also interesting. They attain their highest growth in the bear, next in *Zalophus*, then *Callorhinus* and least in *Phoca*.

The triangular area on each hemiserebrum located between the cruciate and precruciate fissures and the intercerebral cleft, designated by Mivart as the ursine lozenge and believed by him to be of considerable importance in indicating a phylogentic relationship between the Pinnipedia and the ursine group of carnivora, was developed equally well in *Zalophus* and *Callorhinus*. In *Phoca* it was not observable, although Turner states that in this form it is present but rudimentary and concealed in the mesal fissure of the cerebrum.

The length of the lateral fissure in *Callorhinus* is somewhat unexpected and in relation resembles a continuous lateral and ectolateral of the bear. In the sea lion and *Phoca* the lateral is a relatively short fissure. In all but the bear there is an independent ectolateral fissure but it is not so satisfactorily developed in *Phoca*.

The postrhinal fissure shows an interesting variation in the different forms. In *Callorhinus* and *Zalophus* it has no connection with the rhinal or Sylvian, but it is a direct continuation of the subfissure—postica. In *Ursus* the subfissure may occasionally reach it but as a rule it is distinct and the postrhinal continues as an elongation of the rhinal. In *Phoca* the separation of the subfissure and the postrhinal is still more marked, so that the rhinal and the postrhinal are practically different parts of one and the same fissure, differentiated from each other by the presence of the Sylvian.

The presupersylvian fissure is directly continuous with the supersylvian in *Ursus*, it is likewise continuous in *Zalophus* and

in *Callorhinus* except upon the left hemiserebrum of the pup. In *Phoca* the two fissures are distinctly separated

The postsupersylvian is continuous with the supersylvian in *Ursus* and *Zalophus* but separated in *Callorhinus*. They are apparently continuous in *Phoca*, but a dorso-caudal branch and the presence of submerged buttresses at this point of junction would indicate that there was some attempt at separation.

In the bear there is no elongation of the paracoele to form a postcornu; in the sea lion Murie finds a distinct postcornu present; in *Callorhinus* it is quite rudimentary; in *Phoca* Tiedemann represents the paracoele with no appearance whatever of a postcornu. My own specimen, which so far as I know is normal, shows a postcornu relatively as large or larger than in the primate brain with a distinct calcar or hippocampus minor in which a portion of the splenial appears as a total fissure.

With the exception of the bear, concerning which I have no 'data, and the additional brain from an adult *Callorhinus* and *Monachus* all of my material was from specimens not more than one year of age. It is believed, judging from a comparison of the brain of the young with that of the adult *Callorhinus* as to bulk and complexity of fissuration, that comparatively little or no change occurs, especially in the latter respect.

Mr. Lucas, who had casts of the cranial cavities prepared from the male and female fur seal, finds but slight difference in the size of the cavities, notwithstanding the fact that the bulk of the body of the male is about four times as great as that of the female. Of the representatives of the five groups examined, the brain of *Callorhinus* shows a greater number of minor fissures and a more intricate arrangement and branching of larger fissures. With regard to the ground plan of the fundamental fissures, and allowing for the difference in the shape of the brains, that of the eared seals, *Callorhinus* and *Zalophus*, approximates in general more closely to that of the ursine carnivora than does *Phoca*. The latter, or earless seal, in some respects, appears aberrant. The arrangement of the cruciate and postrhinal fissures would seem to link it with the canine and feline carnivora; while the peculiar development of the occipital region and the large development of the postcornu with its calcar point toward primate conditions. The group of lemurs is also said to possess a postcornu and to have affinities with both the carnivora and the primates. As a matter of convenience a table of the more interesting regions in the representatives of the different groups examined is herewith appended.



<i>Region.</i>	<i>Ursus.</i>	<i>Zalophus.</i>	<i>Callorhinus.</i>	<i>Monachus.</i>	<i>Phoca.</i>
1 Subfissure postica (?)	present	present	present	not very distinct	present
2 Postrhinal	Continuation of rhinal, exceptionally postica	Continuation of postica	Continuation of postica	A mere trace, very superficial connection with postica	Continuation of rhinal
3 Presupersylvian	Continuous with supersylvian	Continuous with supersylvian	On left hemicerbrum of pup disconnected but usually continuous	Connected with supersylvian	Disconnected
4 Postsupersylvian	Continuous with supersylvian	Continuous	Disconnected	In four hemicerbrums two show a connection and the other two a disconnection	Continuous but some indication of a shallow
5 Precruciate	mostly dorsal	Dorsal	Dorsal	Mesal and dorsal	Not clearly shown
6 Cruciate	Dorsal just cutting mesal margin	Dorsal	Dorsal	Dorsal and mesal	Dorsal and mesal
7 Postcruciate	Present	Present	Present	Rudimentary	Present
8 Minor fissures	Rare	not many	numerous	quite numerous	quite numerous
9 "Ursine Lozenge"	present	present	present	small	absent
10 Postcornu	absent	small	small	large	very large
11 Calcar	absent	absent	absent	Indistinct	very distinct
12 Medilateral fissure	present	present	present	present	a series of small disconnected fissures
13 Marginal fissure	absent	present	present	a series of short interrupted fissures	present
14 Collateral fissure	absent	rudimentary	present	present	present but connected with postrhinal
15 Insula	slight	slight	slight	slight	slight



## DESCRIPTION OF PLATES.

## REFERENCE LETTERS.

<i>ans.</i> .—ansate fissure.	<i>pcr.</i> .—postcruciate fissure.
<i>b.</i> .—buttress.	<i>pl.</i> .—plexus.
<i>cal.</i> .—callosum.	<i>prc.</i> .—precornu.
<i>calc.</i> .—calcar.	<i>prcr.</i> .—precruciate fissure.
<i>cf.</i> .—confinis fissure.	<i>prh.</i> .—postrhinal fissure.
<i>cl.</i> .—callosal fissure.	<i>prsp.</i> .—presplenial fissure.
<i>col.</i> .—collateral fissure.	<i>prss.</i> .—presupersylvian fissure.
<i>cor.</i> .—coronal fissure.	<i>psp.</i> .—postsplenial fissure.
<i>cr.</i> .—cruciate fissure.	<i>ps.</i> .—postsupersylvian fissure.
<i>cl.</i> .—ectolateral fissure.	<i>r.</i> .—rostral fissure.
<i>f.</i> .—fimbria.	<i>rh.</i> .—rhinal fissure.
<i>g.</i> .—genual fissure.	<i>so.</i> .—superorbital fissure.
<i>hip.</i> .—hippocampus.	<i>sp.</i> .—splenial fissure.
<i>l.</i> .—lateral fissure.	<i>str.</i> .—striatum.
<i>marg.</i> .—marginal fissure.	<i>Syl.</i> .—Sylvian fissure.
<i>mc.</i> .—medicornu.	<i>ss.</i> .—supersylvian fissure.
<i>ml.</i> .—medilateral fissure.	<i>th.</i> .—thalamus.
<i>pc.</i> .—postcornu.	<i>ur.</i> .—ursine lozenge.

## PLATE X.

*Fig. 1.* The ventral aspect of the brain of the fur seal *Callorhinus ursinus*. On each side of the cerebellum is a depression into which fits the petrosal portion of the temporal bone.

*Fig. 2.* The dorsal aspect of the brain showing the cerebellum largely concealed by the cerebrum.

*Fig. 3.* The left lateral aspect of the cerebrum of a young specimen.

*Fig. 4.* The right lateral aspect of the cerebrum of an adult male *Callorhinus*.

*Fig. 5.* The mesal aspect of the right hemicerebrum.

*Fig. 6.* The mesal aspect of the left hemicerebrum.

## PLATE XI.

*Fig. 1.* The ventral aspect of the brain of the haired seal, *Phoca vitulina*, slightly modified from Tiedemann's figure.

*Fig. 2.* The dorsal aspect of the cerebrum of *Phoca vitulina*, after Tiedemann.

*Fig. 3.* The left lateral aspect of the cerebrum.

*Fig. 4.* The right lateral aspect of the cerebrum.

*Fig. 5.* The mesal aspect of the right hemicerebrum.

*Fig. 6.* The mesal aspect of the left hemicerebrum.

## PLATE XII.

*Fig. 1.* The left lateral aspect of the cerebrum of the sea lion, *Zalophus californianus*.

*Fig. 2.* The right lateral aspect of the cerebrum of *Zalophus*.

*Fig. 3.* The mesal aspect of the right hemicerebrum.

*Fig. 4.* The mesal aspect of the left hemicerebrum.

*Fig. 5.* The left lateral aspect of the cerebrum of *Ursus thibetianus*.

*Fig. 6.* The mesal aspect of the right hemicerebrum of *Ursus*.

*Fig. 7.* Dissection of the left hemicerebrum of *Callorhinus*, showing the lateral ventricle with a very rudimentary postcornu.

*Fig. 8.* Dissection of the left hemicerebrum of *Phoca vitulina*, showing the presence of the calcar and large postcornu in the lateral ventricle.

*Fig. 9.* Dissection of the right hemicerebrum of *Monachus tropicalis* showing a postcornu of intermediate size.

## PLATE XIII.

*Fig. 1.* The ventral aspect of the brain of a female *Monachus tropicalis*.

*Fig. 2.* The dorsal aspect of the brain of a female *Monachus*.

*Fig. 3.* The left lateral aspect of the brain of a male *Monachus*.

*Fig. 4.* The right lateral aspect of the brain of a female *Monachus*.

*Fig. 5.* The mesal aspect of the left half of the brain of a female *Monachus*.

## THE CORTICAL MOTOR CENTRES IN LOWER MAMMALS.

By C. L. HERRICK.

WITH PLATE XIV.

Two recent papers relating to the excitable zone of the cortex of the opossum recall an extended series of experiments made by the writer prior to 1892 but which have been published only in part and seem to have failed to reach the public for whom they were intended.

R. H. Cunningham<sup>1</sup> remarks: "To be sure, the microscopical as well as the macroscopical anatomy of the opossum brain has been minutely described by Herrick, who regards the precrucial lobe as typically motor in its microscopical structure and the parietal and occipital portions as composed of motor and other nerve cells, but this writer does not state whether this view has been corroborated by a physiological investigation of the cortex with the electrical current." The writer must admit that he has often failed to take the usual steps to bring his papers to the attention of fellow workers (though reference is made to experiments in the paper quoted) and it may be that the fact that Professor Cunningham as also Professor Ziehen<sup>2</sup> overlook the observations referred to, is due to in part to this negligence. That part of the series not heretofore published has been withheld in the hope that an opportunity might yet arise for the completion of the contemplated series. The preliminary account appeared in the paper prepared jointly by Professor W. G. Tight and the writer and printed in the Bulletin of the Laboratories of Denison Univer-

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<sup>1</sup> The Cortical Motor Centres of the Opossum. *Journ. Physiology*, XXII, 4.

<sup>2</sup> Ueber die motorische Rindenregion von Didelphys. *Centralblatt für Physiologie*, XI, 15.

sity, V. 1890.<sup>1</sup> The paragraphs immediately germane are the following:

“Previous to the sectioning, as already said, several localization experiments were made both by electrical stimulation and extirpation. The first specimen was a male of *Arctomys monax*, the same specimen which furnished the sections most frequently described and figured beyond. Ether was employed as an anesthetic, and the skin was parted down the median line of the head and the skull removed over the anterior and middle parts of the left hemisphere. The current used was from one Grove cell and was just enough to operate the induction coil, producing an irritation easily endured by the tongue. When the electrodes were introduced at *a*, Fig. 4, Plate V (at about the anterior one-third, near the median line and corresponding approximately to Munk’s region C of the dog) a forward and outward motion of the right fore leg was produced. A stronger current produced an electro-tonic contraction of the muscles of the whole right side. At the point *b*, about 5 mm. behind and a little outward from the above (corresponding to about the posterior margin of Munk’s region D), the stimulus produced a straightening of the right hind leg. At the point *c*, about 8 mm. behind *b*, and near the median fissure (corresponding to about Munk’s region F, near the median line), the stimulation resulted in a sharp contraction of the orbicularis palpebrarum and orbicularis oris of the right side and some feeble contraction of the facial muscles of the left side, probably due to superficial irradiation.

“At the point *d*, about 8 mm. behind *c*, and farther from the median fissure (corresponding to the anterior margin of Munk’s region A), the insertion of the electrodes produces no motor disturbances nor did any point back of *d*. By a series of trials it was found that the electrodes produced some motor disturbance of the fore leg at all points within the area marked A, but not beyond it.

“The area B likewise marks about the limits of the hind leg

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<sup>1</sup> The Central Nervous System of Rodents, etc.



region. An area of about 5 sq. mm. was then removed from the cortex of the left side of the fore leg region at about *a*. The wound was then dressed and the animal allowed to recover. The power of abduction of the right fore leg was lost. After some time another portion of the cortex was removed, a little back of *d*, on the left side. After recovery it was found that the animal was blind in the right eye. These experiments serve to locate some of the motor and sensory regions of the cerebral cortex for the subsequent histological works.

"It may be of interest to note also one of the series of experiments of electrical stimulation upon the Raccoon, *Procyon lotor*, which has been employed for comparative study. The animal was a male about three-fourths grown. Just enough current was used to drive the coil. Ether and choloform mixed were the anesthetics employed.

"Nearly the whole upper surface of the cerebral hemisphere of the left side was exposed. The loss of blood was very moderate.

"The electrodes were introduced at point 1, Fig. 2, Plate XI, about 9 mm. from the median fissure and a little in advance of the line passing through the anterior angle of the eye. The result was a forward and inward motion of the right fore leg.

"At point 2, the introduction of the electrode gave an undefined movement of the right fore leg.

"At point 3, about 7 mm. from the median line and separated from 1 by a faint sulcus, the stimulation produced a flexion of the pes on the crus and elevation of right hind leg.

"At 4, a movement of the right hind leg, as at 3, and a slight rotation of the fore leg inwards.

"At 5, about 3 mm. from the median line, the stimulation produced an extension and divarication of the digits of the right foot.

"At 6, the fore leg was elevated and flexed, and with a little stronger current the hind leg was also elevated and flexed.

"At 7, there was an extension of the toes corresponding to the movements produced at 5, of the opposite side.

"Perhaps more important in its bearing on the present subject is a set of experiments upon the opossum, of which, unfortunately, no very exact data have been preserved. The configuration of the hemispheres as well as the details of structure resemble very closely those of rodents. Moreover, such hints as we have of the development of the Rodentia indicate a common origin for the two groups and comparatively slight subsequent differentiation. It, then, would not be surprising if a considerable similarity of distribution in the cortical elements should be proven to exist. On the other hand, the existence of an apparent homologue of the crucial sulcus near the front of the cerebrum would lead one to expect the aggregation of the motor elements near this sulcus. The experiments in this case were made with a Grenet cell and DuBois-Reymond coil, with the secondary coil at about 8 cm. the current being applied by a pair of platinum electrodes separated by about 3 mm. Stimulation of the region about the crucial sulcus (so-called) resulted in movements of the anterior extremity, but the difficulty in controlling the flow of blood interfered with close analysis. The area on either side of the median fissure responded with various poorly localized contractions of the trunk. About 6-8 mm. posterior to the crucial sulcus and 4-5 mm. from the medial line is an ill-defined area governing the hind leg. These motor reactions were, in the main, crossed as usual, but in several instances similar motions of the muscles of both sides resulted when superficial irradiation appeared to be excluded. The areas thus roughly mapped in the opossum coincide in general with those of the ground hog and we are forced to conclude that the crucial sulcus of the opossum is not strictly homologous with the fissure so named in carnivora."

Cunningham locates the motor centre for the fore limb along the caudal boundary of the so-called crucial sulcus and doubtfully reports an area for movements of the ear in the lateral region, pretty well caudad. He states that there is no definite centre for the hind leg or, at least, that if the animal is thoroughly under the influence of the narcotic no motion can be evoked by electrical stimulation. Ziehen, on the other hand,

locates the hind-leg region behind the "crucial sulcus" about at the point devoted by Cunningham to the flexion of the toes of the fore foot. He adds however that this region is less easily excitable than the others. Ziehen is also struck by the fact that his results reverse the relation between the fore and hind leg regions as compared with the rodents and insectivora. On the other hand, our own results, so far as they go, are in harmony with what we know of other groups, although this method of localizing the cortical areas is, we believe, open to grave objections from the theoretical as well as the practical standpoint. It is no unusual thing for an animal that seems to be fully under the influence of the narcotic to respond in the most distinct and apparently localized manner to stimuli at the most unexpected points, as a result probably of general irritation. An illustration of this is afforded by the raccoon brain of figure 2. The cortical area indicated on the right side was first extirpated. Before recovery from the narcosis there was a tendency to rotate toward the right, i. e., the side of the injury. After recovery the animal seemed quite blind on the opposite side. He would snap at a stick or flinch from a threatening blow when within the field of the right eye, but quite ignored the same movements on the other side. A day later there seemed to be no irritation and the pupil reflexes were normal. The loss of sense of touch of the left fore leg was quite evident, though hard to differentiate because of the loss of vision. Subsequently the left hemisphere was exposed and stimulation experiments were attempted in the usual manner but which proved quite uncertain. Nevertheless, the areas in which are found the points numbered 1, 4, 8, and 13 presided over the motions of the hind leg and foot. This area is somewhat farther caudad than the hind leg area described in the raccoon in the experiments quoted above but in the same general region. Regions further laterad both in front and behind the area mentioned occasioned motions of the fore foot and leg.

Fig. 3 gives a few data from stimulation experiments with a kitten. Here points 4 and 5 are devoted to the hind leg, 3

and 2 to the fore leg and 1 is on the border between the two regions.

A large series of stimulation experiments on the musk rat (Fiber) are passed over as wholly ambiguous or contradictory. Fig. 4, *b* illustrates a case of extirpation in this subject. Previous electrical stimulation of the cephalic part of this area resulted in motions of the fore foot for the most part. After recovery from the operation there was very evident impairment of the power of abduction in the manus and pes of the right side. When pushed towards the right the animal offers no resistance and may be turned upon its back, while the effort to push it toward the left is met by decided resistance. Tactile sensation is also weakened on the right side, as shown by the reaction to the needle. A second specimen was deprived of the cortex within the fore-leg region and, after recovery, some impairment of the motion of the opposite fore-leg was apparent. The animal seemed unable to extend the fingers and the fingers double under while walking. It is easy to push the animal over toward the injured side. On the other hand the coördinated motions like those of washing the face are carried out without difficulty. In another specimen a larger area was removed extending further caudad. Fig. 4, *c*.

The symptoms were much the same except that there is a greater apparent involvement of the hind limb. Loss of muscular sense is suggested. The power of adduction seems to have suffered most. After 10 days recovery is nearly complete, at least so far as locomotion is concerned, but there is a curious awkwardness, hard to describe but easily recognized. When sitting up it tends to fall toward the side opposite to the lesion. Vision was permanently destroyed in the eye of the opposite side. After 20 days all efforts to provoke motion result in rotation to the right. This is due, in all probability, to the extension of the effect of the injury by inflammatory processes. In yet another case in which the same area was removed the rotation began soon after the operation and continued till it terminated in convulsions. The animal was blind in the opposite eye.



## EXPLANATION OF PLATE V.

*Fig. 1.* Dorsal aspect of brain of *Didelphys virginiana*; 1, point where fingers of left hand were extended and divaricated; 2, left leg moved cephalodorsad; 3, fingers of left manus extended and divaricated; 4, extension of right manus; 5, same as 1.

*Fig. 2.* Dorsal aspect of brain of *Procyon lotor*. Extirpated area of right hemisphere shaded. See text. The numbers on the figure not referred to in the text indicate places the stimulation of which was followed by no definite reaction.

*Fig. 3.* Dorsal aspect of brain of half-grown *Felis domestica*; 1, flexure of pes and contraction of shoulder muscles; 2, extension of left manus and forward motion of arm; 3, inward rotation of left manus; 4, forward motion of left hind leg; 5, flexure of toes of right pes.

*Fig. 4.* Brain of *Fiber zibethicus*; *b*, areas extirpated. See text.

*Fig. 5.* Localization in Opossum brain according to Ziehen. *H*, hind leg; *F*, fore leg; *Mf*, mouth-facial region.

## THE NERVE CELL AS A UNIT.<sup>1</sup>

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WITH 7 TEXT-FIGURES.

The sciences of morphology and physiology, perhaps more than any others, were of slow development. Their early years were enshrouded in mysticism and magic. Progress was retarded largely by theological opposition associated with superstition. The ancients believed that the soul was slow in leaving the body and that the latter should not, therefore, be used for dissection at once. The period allotted for this migration of the soul, left the body in anything but a fit state for investigation. This opposition did not extend to chemistry and other sciences, which, at that time, were in a flourishing condition.

With the *renaissance* there came a renewed interest in anatomy, and in Italy it was decreed that *one* body should be dissected annually at the universities. This, curiously enough, was done by a barber's assistant with a razor.

There was a time when it was the custom to administer to the inner, as well as to the outer, ills of mankind. Barbers were particularly adept at bleeding, and combined the science of phlebotomy with that of shaving. To advertise this profession they erected signs in the form of poles wrapped around with red and white bandages—the red to indicate the bleeding, and the white, the soapy lather. We must, doubtless, look upon our modern barber poles as heirlooms of this ancient and honorable profession, deprived, to some extent, of their old time significance.

Because the sphere was accepted as the symbol of perfection by the ancients, Plato regarded the more or less globular

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<sup>1</sup> Read at the quarterly meeting of the Cayuga County Medical Society, Auburn, N. Y., Feb. 10, 1898.

head as the seat of intelligence and perception. With slow gradations the apparent fantastic and irregular form of the wrinkled brain surface has been systematized into a general ground-plan. Segments have been differentiated and a fissural pattern for the cerebrum has been formulated. Deeper than the surface, however, there is encountered a bewildering maze of cells and fibers, the intricate arrangement and complex relations of which have at the present time, only begun to be understood.

In the achievement of a great discovery, many are prone to overlook the factors by means of which it is made possible. The discovery of a new planet very justly brings great renown to the discoverer,—we usually stop at that and take no cognizance of the wonderful mechanism of the telescope, the laws of astronomy, and other accessories that co-operate in the grand result. And so it has been with our knowledge of the structure of the nervous system, great as it is today but at the same time inadequate. The results of the last ten years which have so completely revolutionized our conceptions of the nerve elements were possible only through improvements in microscopical apparatus and technique, and the improvement of histological methods. With the additional knowledge gained from the new methods, there must of necessity occur change in the terminology. The old notion of a nerve cell (justified by the old methods) that it consisted merely of a cell body with its enclosed nucleus and nucleolus is no longer tenable. Important as are these parts to the nutrition and activity of the cell, no less important to the full attainment of its function is the presence of its various appendages.

The Golgi-Cajal method is too well known to require any description. The formation of a silver-bichromate deposit in or upon the nerve cell and its processes has furnished us with pictures of these elements, which for beauty and clearness of outline surpass anything that has preceded it. The results furnish us with at least a workable hypothesis regarding nervous phenomena which before was merely conjecture.

This method has shown, and accumulated evidence seems

to confirm it, that there is complete morphological independence of the nerve elements, with perhaps certain exceptions, in rare cases, where a direct anastomosis of one nerve cell with another has been described, as in the battery of the torpedo and also in certain of the sense organs, as noted by Dogiel, Ayers, Masius and others. This morphological isolation of the elements does not preclude the idea of physiological continuity which must of necessity exist.

This isolation of elements has led to the production of the term neuron (Waldyer '91), neurone (Van Gehuchten '93), neurocyte (Fish '94, after an unknown French writer), neura (Raubert '94) and neurite (Baker '96), to signify the nerve unit, including the cell body with all its appendages. The term neurocyte has been suggested in this connection because its literal meaning is a nerve cell and includes not merely the cell body, which from custom we regard as the equivalent of a nerve cell, but all of its appendages as well, just as in speaking of the leucocyte, we include the various extensions from the cell mass. The analogy may be carried still farther for under certain special conditions we may conceive that the pseudopodia of the leucocyte may be considerably extended and attenuated and from the juxtaposition of numerous other elements lose, or partially lose, their powers of retraction and movement; under such conditions we may consider the neurocyte comparable with the leucocyte so far as form is concerned.

The appendages of the cells, with perhaps the exception of those of the spinal ganglia, appear to fall naturally into two categories; those which collect or convey the impulse to the cell, cellipetal processes or dendrites, and those which discharge or carry impulses away from the cell, the cellifugal processes or neurites (axis-cylinders).

Along with our increasing knowledge of the form of neurocytes there have been contributed new facts bearing upon their activity. For our purpose, we may consider the neurocyte as made up of a mass of granular protoplasm, with more or less branching appendages, containing a large nucleus of a reticulated character enclosing, usually, a prominent nucleolus. We



have a bit of material protoplasm similar to that of other body cells, and yet for a long time any structural change due to the activity of the nerve cell eluded the keen vision of investigators. It has been said that the secretion of a gland cell is of a material character; that of a muscle cell, mechanical energy and we might naturally expect to find in these tissues, changes demonstrable by the microscope; but the secretion of a nerve cell is consciousness which is not exactly material, and its effect upon the cell is too subtle to leave a trace. Hodge<sup>1</sup> in his fatigue experiments extending over a period of four or five years, has shown the fallacy of this view. His experiments dealing with artificial and normal fatigue were performed in a most faithful and conscientious manner on a wide range of forms with conclusive results, the most of them having been confirmed by later investigators.



Fig. 1.



Fig. 2.



Fig. 3.

*Figs. 1, 2 and 3, after Hodge.* Only the cell bodies are shown. Fig. 1, represents the normal cell body with its large reticulated nucleus and the chromatin diffused throughout the cytoplasm. Fig. 2, shows the effects of fatigue, the nucleus having become shrunken and irregular in outline, with a surrounding area devoid of chromatin. The peripheral portion of the cytoplasm is also poor in chromatin. Fig 3, showing vacuolation of the cytoplasm as the effect of fatigue.

For the artificial fatigue experiments the spinal ganglion cells were chosen and the nerve connecting with the ganglion was subjected to a weak electrical stimulation for a given length of time. The spinal ganglion of the opposite side was removed *without* stimulation and used as a control in the experiment, the treatment of the two ganglia being identical after they were removed from the body. In the fatigued cells he found slight shrinkage in size, with vacuolation of the protoplasm. In the nucleus there was a marked decrease in size, nearly 50%; a change from a smooth and round to a jagged, irregular out-

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<sup>1</sup> Jour. Morphology. Vol. VII. Pages 95—164. 1892.

line; and a loss or condensation of the open reticulated appearance. The control ganglion showed none of these changes. If, after stimulation, the cells were permitted to rest and then examined, these changes were not apparent. For the study of normal fatigue, certain birds and bees were examined, some of them were killed before entering their daily routine, while their cells were presumably as yet in a state of rest; others were killed just at night-fall after the completion of their day's work. A comparison of those killed in the morning with those killed in the evening, showed in the latter changes as marked as those produced by artificial fatigue. To make the evidence still stronger, and to show that the effects were not the result of histological reagents, it remained for Dr. Hodge to study the living cell. For this purpose he chose the cells of the sympathetic ganglia of the frog. Two frogs were prepared in exactly the same way, except that one received a weak electrical stimulation while the other did not. The unstimulated frog showed no change, while the nucleus of the cells of the stimulated frog showed very marked shrinkage and irregularity of outline. Certain well defined changes in the constitution of the nerve cells of very old persons as compared with the newly born have also been demonstrated. Hodge has shown that fatigue effects occur in brain cells as well as those of the spinal ganglia.

As early as 1884, Flesch noted differences in cells in their reaction to staining reagents due to internal modifications as an effect of their functional activity, and according to this affinity for color he designated the cells as chromophile and chromophobe.

Vas ('92) has demonstrated changes in the cells of the cervical ganglia, due to their functional activity, and confirms, in the main, the points that have just been stated. As a preliminary result of this activity Vas has further noted that there is, at first, a swelling of the cell. This has also been confirmed by Mann ('94) who has extended the observations to the motor cells of the spinal cord and the sensory cells of the retina of the dog. From his researches, Mann concludes that during rest,

several chromatic materials are stored up in the nerve cell and that these materials are used up by it during the performance of its function ; that activity is accompanied by an increase in the size of the cells, the nuclei and the nucleoli of the sympathetic, ordinary motor and sensory ganglion cells ; that fatigue of the nerve cell is accompanied by the shriveling of the nucleus and probably also of the cell and by the formation of a diffuse chromatic material in the nucleus. Lugaro ('95) confirms the observations of Mann.

Cellular changes of such a radical character, as has been shown above, may be the result of perfectly normal functions and disappear after a period of rest. How important is it, then, before discriminating between that which may be perfectly normal and that which is abnormal, to know thoroughly the effects incident to natural activity.

In connection with the matter of electrical excitation of the nervous system, the question naturally arises, since we have such complete evidence from an experimental standpoint, what will be the result of the application of a fatal current of electricity? Will a very strong current applied for a few minutes affect the structural character of the nerve cells in a manner similar to those stimulated by a weak current for a very long time? As opportunities have presented there have come to me portions of the brain and myel of four persons executed by electricity, as well as from a horse struck dead by a live wire. In the first case, designated as W, a portion of the oblongata, the location of so many vital centers, was carefully studied. The number and size of the vacuoles in the cytoplasm were astonishing. In all, however, the nucleus appeared full and regular, although the cytoplasm in some of the cells seems to have become completely transformed into vacuoles.

In the second case, L, examination was made of the same region and here no abnormal change of any kind could be detected. The cells were full and plump as were also the nuclei and the nucleoli, and the cytoplasmic chromatin showed no evidence of disintegration or disappearance. A portion of the cortex was also examined and in both the large and the small

pyramidal cells a very considerable amount of vacuolation appeared, especially in the apical dendrites, and occasionally in the body of the cell.

In the third case, B, only a small portion of the cerebellum was studied. It required considerable search and patience to find in these sections any distinct structural change of the cells. After the examination of many sections two Purkinje cells were found, each of which showed the presence of a small vacuole.

The fourth case, C, required more than one current to cause his death. The pyramidal cells of the cortex were also examined and those of the oblongata to a lesser extent. Here also there was evidence of vacuolation in the apical dendrites of the pyramidal cells, while the others, including those of the oblongata, so far as examined, were perfectly normal.

In the case of the horse the injury was inflicted at the shoulder, differing thus from the others in point of contact with the electricity. No unusual appearances were detected in the neurocytes.

I have ventured to present these results, incomplete as they are. If they do nothing more, they will, I think, emphasize the importance of a working knowledge of the changes that may occur in a neurocyte as a result of its legitimate processes. The vacuolation of the cell body and of the nucleus is described by many to be due to pathological causes of various kinds, among which may be mentioned, insanity, alcoholism, epilepsy, as well as the action of various toxins and alkaloids. As has been shown by Hodge and others, many of the described pathological changes may be duplicated by normal processes, and these, so far as possible, should be eliminated before rendering a decided opinion.

Bearing upon the matter of the rapidity with which effects may be produced upon the nerve cells as a result of shock are recent experiments of Parascondolo ('98)<sup>1</sup> who produced upon guinea pigs a condition of shock by striking some of them upon

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<sup>1</sup> Arch. de Physiol. norm. et path., XXX, 5th series. X. No. 1. p. 138.



the thorax and some upon the abdomen. If the animal died immediately there were no results detected in the nervous system. If, however, the animal lived thirty or forty hours, as some of them did, well marked lesions were demonstrated. By Nissl's method he found in the motor cells of the myel a perinuclear, as well as a peripheral chromatolysis, also vacuoles in the cytoplasm and an eccentric position of the nucleus. By the Golgi method he found deformation of the cell body but not to the extent of atrophy, and a distinctly moniliform appearance of the dendrites.

An inference derivable from the above experiments, is that changes of a structural character do not occur instantaneously in the neurocyte, especially if the injury be not directly applied to the nervous system. Parascondolo's experiments are of interest in showing how soon the lesions may be *induced* through the inter-dependence of the tissue systems. A comparison between these experiments and the results of electrical excitation shows that fatal currents of electricity may *induce* changes in the dendrites of the nerve cells in a practically instantaneous period of time, under unfavorable conditions, as the current is prevented from direct action upon the brain by the presence of the meninges, bones of the cranium, and scalp. With the weaker



Fig. 4.

*Fig. 4.* After Cajal, showing the transformation of the bipolar into the unipolar spinal ganglion cell.

currents practically the nervous tissue alone was dealt with, under the most favorable conditions. Other things being equal, we may expect that a current of greater intensity will produce given results in less time than a current half as great. Pognat<sup>1</sup> has demonstrated this in his experiments, finding that it required

<sup>1</sup> Bibliog. Anat. VI, pages 27-32, 1898.

twice as long to produce certain results with a weak current as when one of twice the strength was used.

We must avoid the danger of regarding the cerebro-spinal axis as a rigid and unyielding mass of substance. The action of the brain is molar as well as molecular, as evidenced by its general movements due to inspiration and expiration. In the earlier stages of development there are migratory movements of the neuroblasts of an amoeboid nature in order that they may reach their destined positions in the adult structure. The so-



Fig. 5.

*Fig. 5.* After Cajal, showing the changes undergone by the cerebellar granule cells, reading from left to right.

called bipolar spinal ganglion cells are the permanent condition in such low forms as the "fishes;" those of higher forms pass from this stage in early development to the unipolar condition of the adult.



Fig. 6.

*Fig. 6.* After Fish (Central Nervous System of *Desmognathus fusca*), showing the changes in the form of the neurocytes as they pass from the ental to the ectal boundary of the layer of nerve cells.

Cajal has shown that during their growth the granule cells of the cerebellum pass through even more elaborate changes than those of the spinal ganglia. Changes in the form of the cells and their appendages are also apparent in the central ner-

vous system of certain salamanders, as the neurocytes reach the boundary of the cellular layer.

Here are evidences of the plasticity of the nervous elements. Do they lose this property entirely after they have reached maturity? It has been pretty well demonstrated by modern histological methods that these elements are morphologically independent, and the hypothesis of *contiguity* or overlapping of the parts is now very generally accepted, instead of the older view of continuity or direct anastomosis of one cell

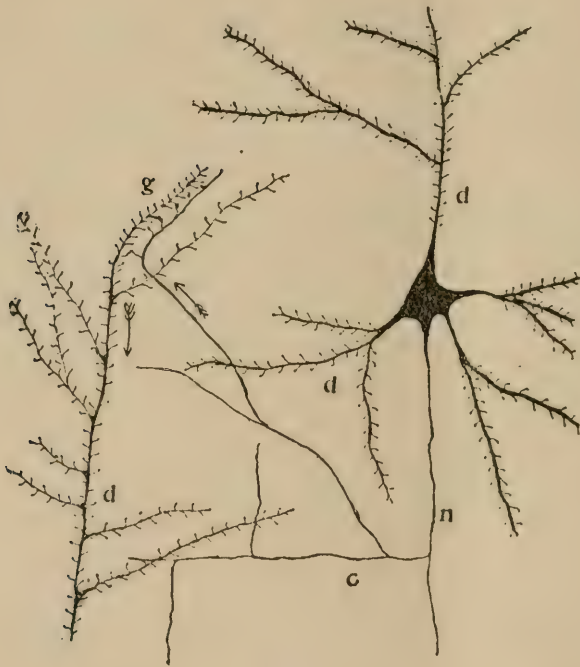


Fig. 7.

Fig. 7. After Berkley, showing a nerve cell with its processes (human); *n*, neurite; *c*, collateral; *d*, *d*, *d*, dendrites; *g*, gemmulæ. Illustrating Berkley's hypothesis of the way in which the nervous impulse may pass from one nerve cell to another by contact of the gemmulæ.

with another. Contact of one element with another is sufficient, it is believed, for the transference of a nervous impulse. The

idea has been advanced that even in the adult state the neurocyte has not completely lost its power of amoeboid movement, but that this property is still retained at the terminals of its appendages. This view is not accepted by Kölliker, nor entirely by Cajal, who thinks that the neuroglia cells are more mobile than the nerve cells.

The experiments upon the activity and fatigue of the nerve cell indicate that a change of volume may occur, a turgescence as a result of activity, and a shrinkage when carried to the extent of fatigue. Situated in the lymph spaces and constantly bathed with the lymph for nutritive purposes, we may expect to find certain osmotic processes going on between the contents of the cell and its surrounding medium and that these processes may be influenced by the activity of the cell and that certain of them may occur coincidently with the transmission or origination of the impulse in the cell.

Along the dendrite, and especially well pronounced in the cortical cells, are slight lateral spurs known as gemmulæ. The condition of these, as well as certain irregularities in the form of the dendrites, have been noted by Berkley and others as the result of pathological causes. Berkley has shown that in certain diseased conditions gemmulæ have been missing. He believes that the cell and its dendrites has a delicate limiting membrane through which the gemmulæ protrude, as naked bits of protoplasm, coming into contact with similar uncovered masses of protoplasm from the neurite or its collaterals, or in contact with the gemmulæ of other dendrites and that at these points the impulses are transferred. Any destruction or abnormality of these gemmulæ would of course, interfere more or less seriously, with the normal conveyance of the impulse.

The transference of nervous impulses from one element to another through contact, due to amœboid movement, would be of material importance in the explanation of the phenomena of sleep, intellectual processes, and pathological conditions. Before pathology has spoken its final word we may hope to know more of the remarkable chemical complexity of nervous tissue, composed, as it is said, of some three hundred or more different ele-



ments and compounds. If, in closing, I could have one fact shine out beyond any other it would be the idea that, while there is a morphological independence of the nervous elements, there is a physiological dependence; that, although there is unity there is community; and that a healthy psychic life is the result of the summation of the individual activity of all the nervous elements.

## EDITORIAL.

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### OUR COLLABORATORS.

Since the publication of our last issue three additional collaborators have been added to our editorial staff. Negotiations are pending with several others both in this country and abroad. We feel that our readers are to be congratulated that they are to have the services of men so eminent in their several departments and representing so many leading institutions of this country and Europe. The staff of collaborators at the present writing includes the following:

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Professor Ludwig Edinger, *Frankfurt, a-M.*, Collaborator for Germany.

Professor A. van Gehuchten, *University of Louvain, Belgium*; Collaborator for France and Belgium.

G. Carl Huber, M.D., *Assistant Professor of Histology and Embryology in the University of Michigan*; The sympathetic system and the peripheral nervous system.

B. F. Kingsbury, Ph.D., *Instructor in Microscopy, Histology and Embryology, Cornell University and the New York State Veterinary College*; Morphology of the lower vertebrates (Ichthyopsida).

Frederic S. Lee, Ph.D., *Adjunct Professor and Demonstrator of Physiology, College of Physicians and Surgeons, New York City*; Physiology of the nervous system.

Adolf Meyer, M.D., *Docent in Psychiatry, Clark University, and Assistant Physician to the Worcester Lunatic Hospital*; Human neurology.

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REPORT ON NEURONYMY BY THE ASSOCIATION OF AMERICAN  
ANATOMISTS.

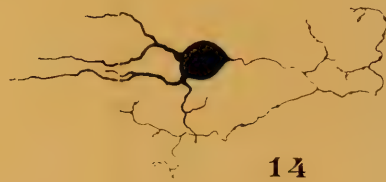
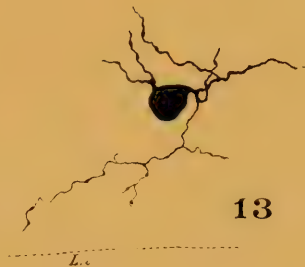
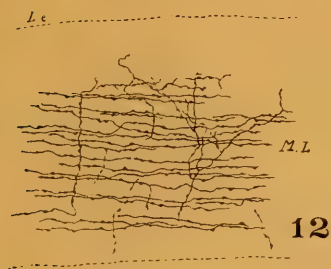
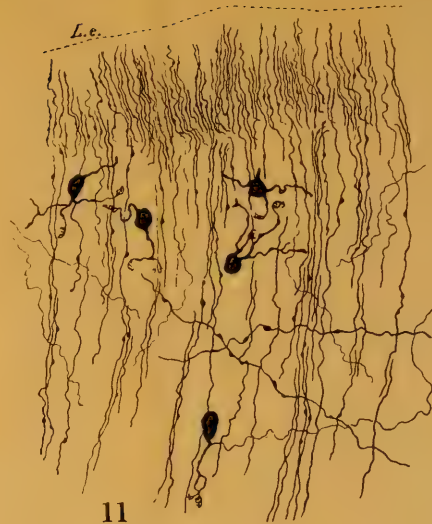
It is much to be regretted that the results of the various attempts to secure harmonious and consistent usage in the terms employed in anatomy and especially neurology have resulted in emphasizing personal differences and producing very unscientific bitterness. It does not increase the attractiveness of a field whose inherent difficulties are only too obvious to discover that its language is broken up into dialects the use of any one of which brands one at once with some "eponymic" adjective of reproach. These remarks are suggested by the appearance of an elaborate report from the Association of American Anatomists accompanied by a caustic minority report involving personal criminations and complaints. The results of the questionnaire recently reported in this Journal are such as to indicate that the system of Professor Wilder is not "repulsive generally to educated men" and such a statement in the organ of a society of national importance betrays an amount of heat without light not calculated, to say the least, to avert the danger that American anatomy should fall into "disgrace." It may be expected that the result of the discussion will be to cause many bewildered writers to adopt *in toto* the only consistent and complete system at present at command while others will react against every idea of reform and thus the breach may become impassible, and for this result we shall have thank the committee of the Association of American Anatomists. For ourselves, we can only advise patience and a careful weighing of the claims of each term apart from any question of source and associations, with reference solely to the interests of our science. Too many problems of first class importance are pressing for solution to permit the student to fritter away time in nomenclature discussions.

C. L. HERRICK.

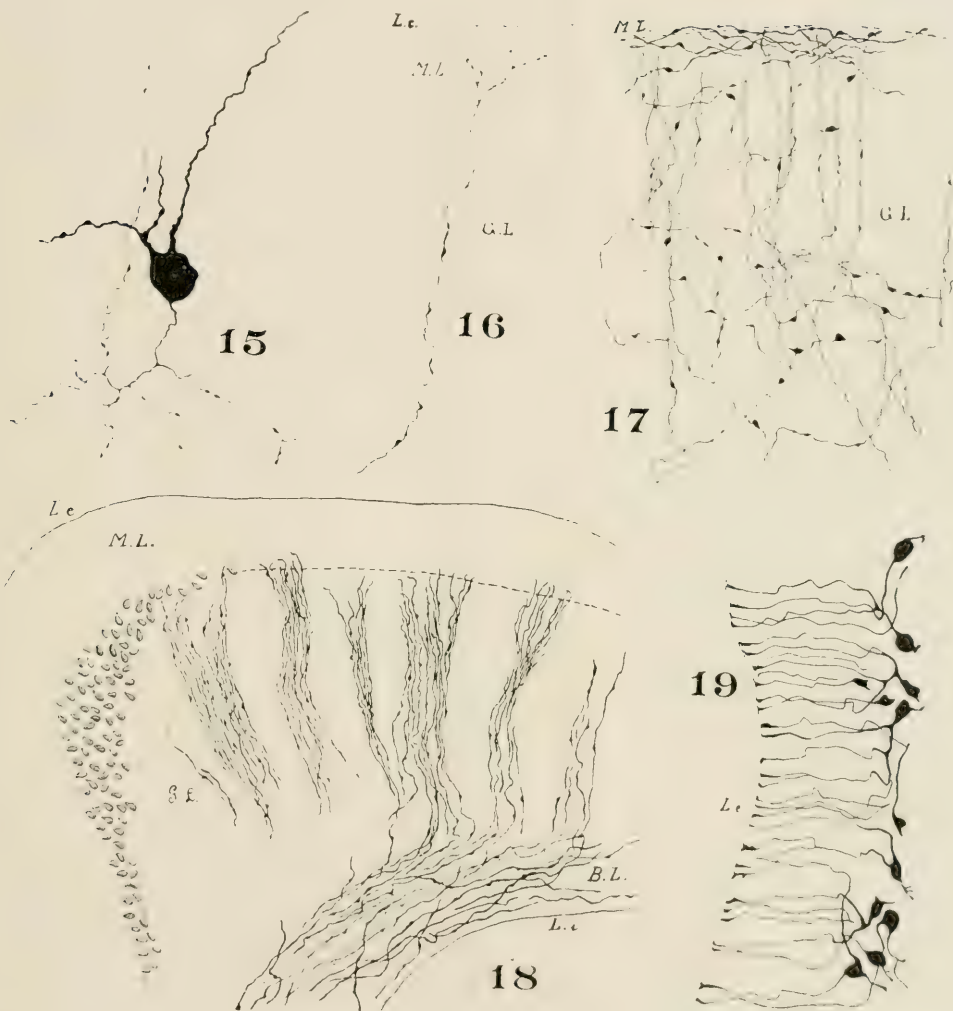






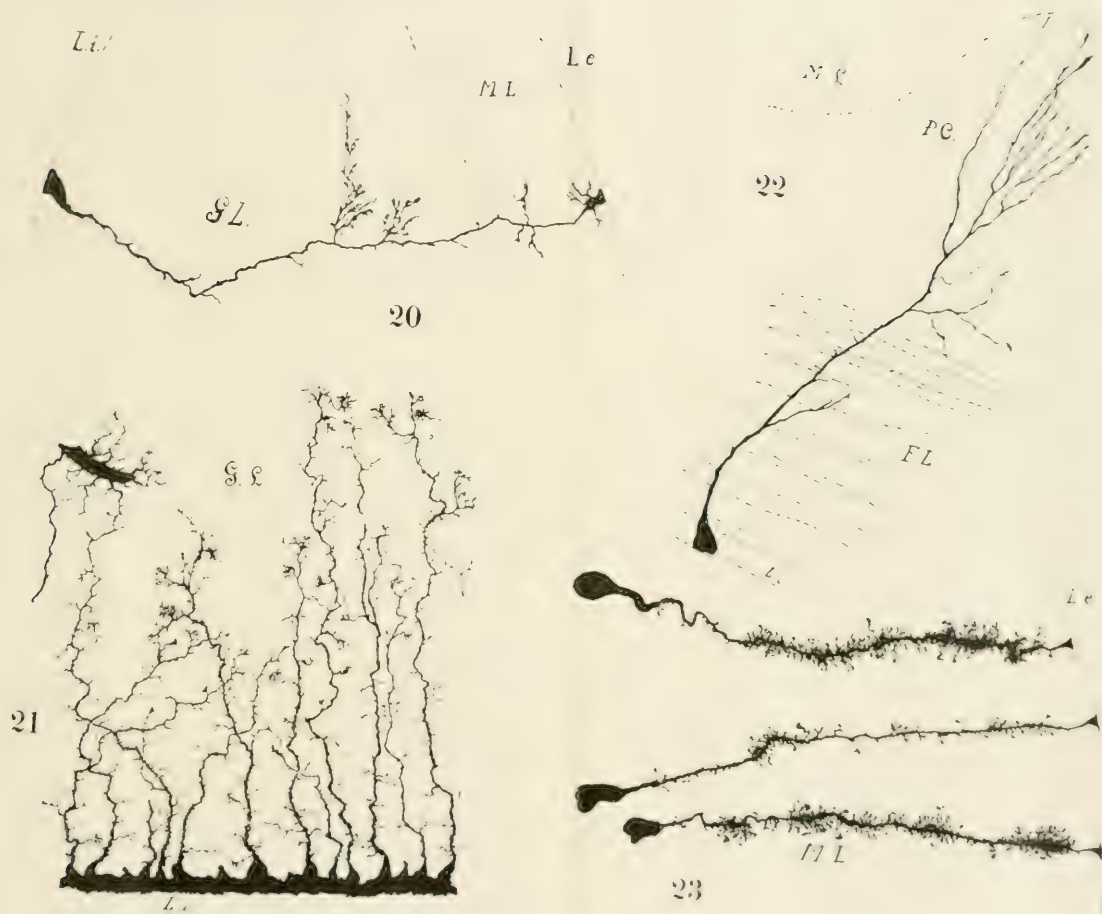




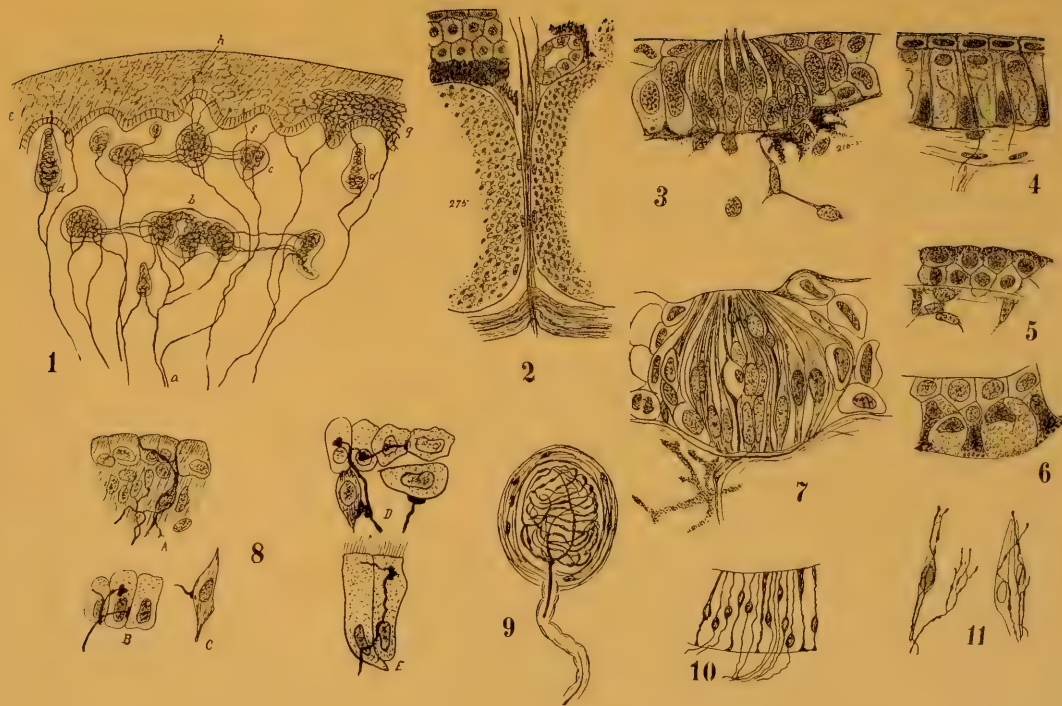






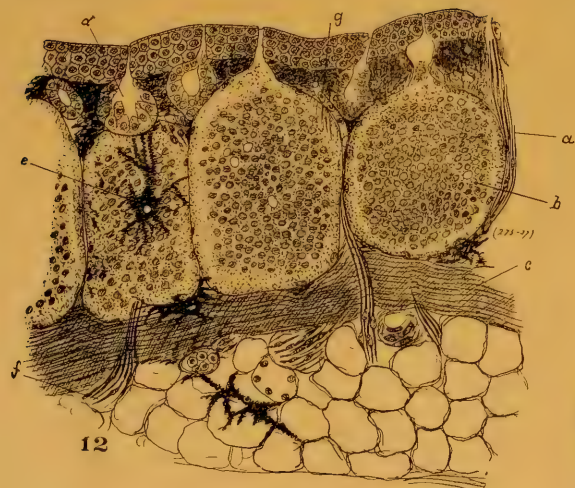












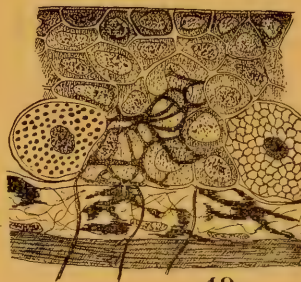
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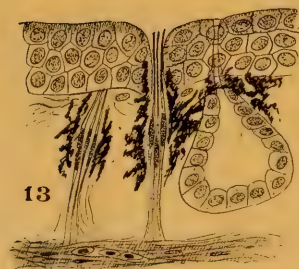
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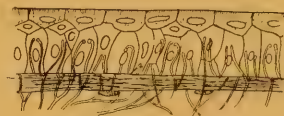
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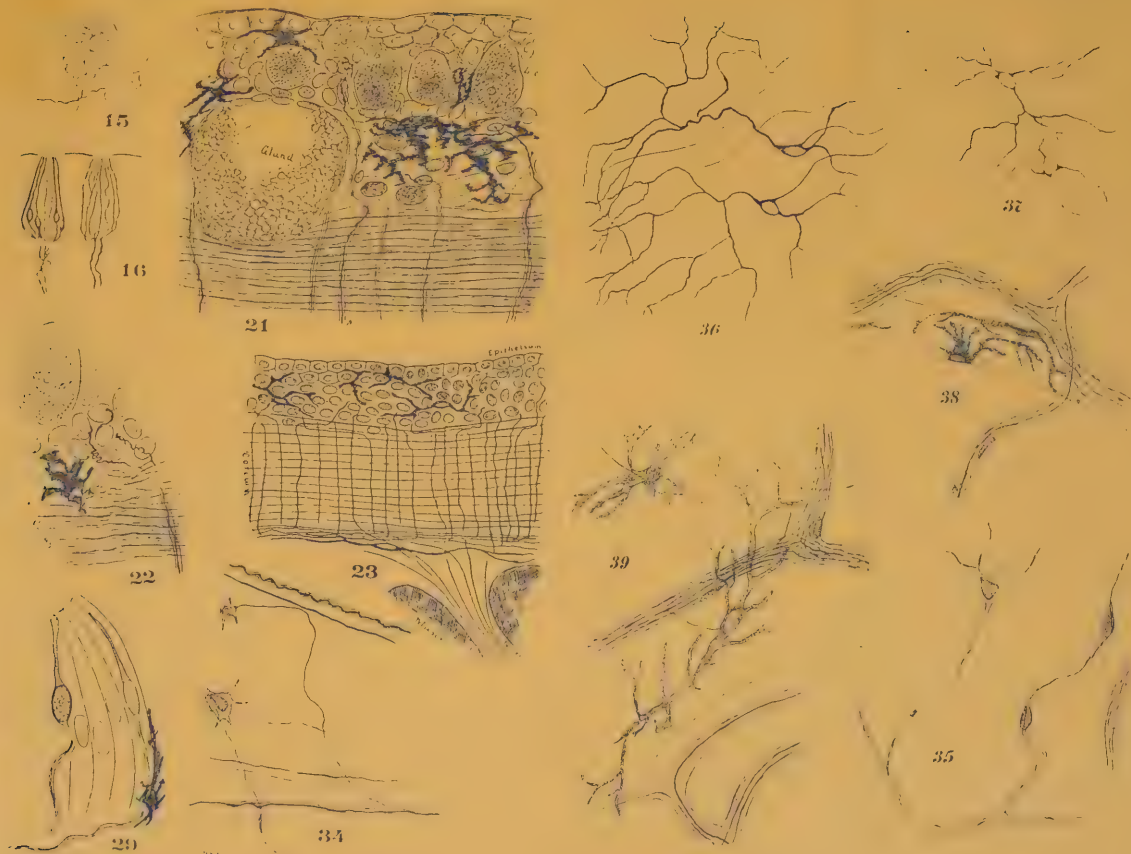
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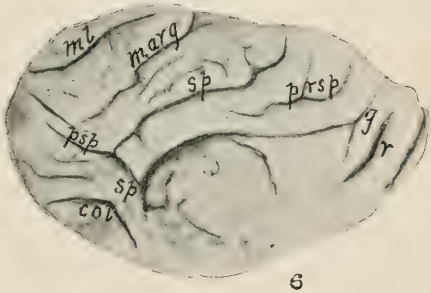
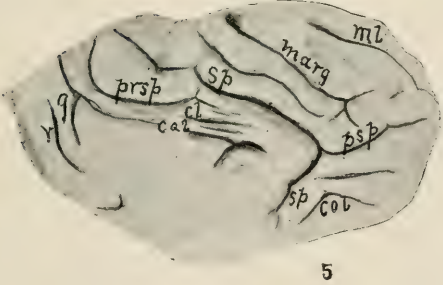
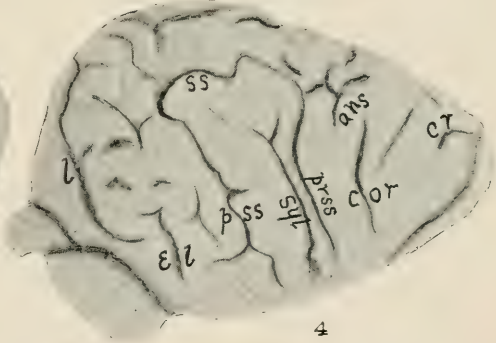
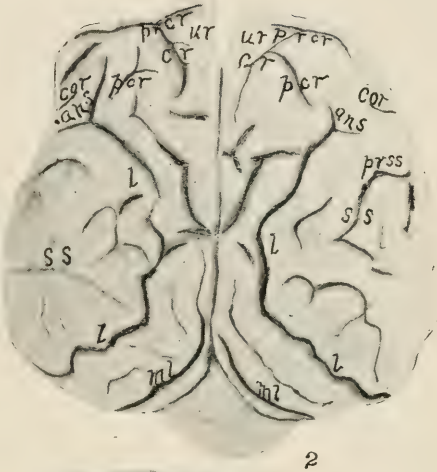
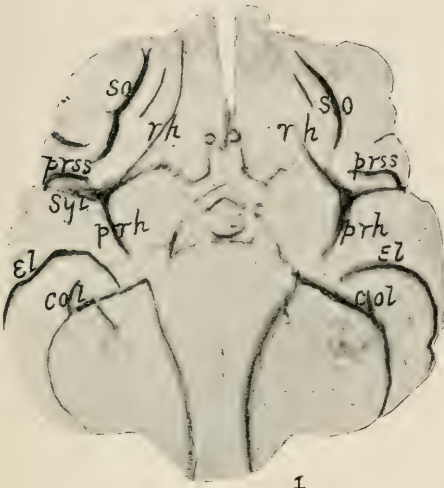
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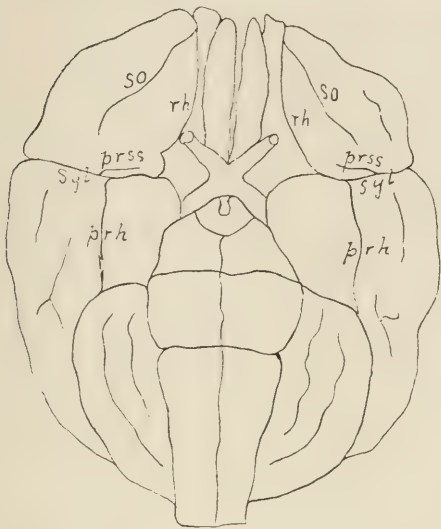
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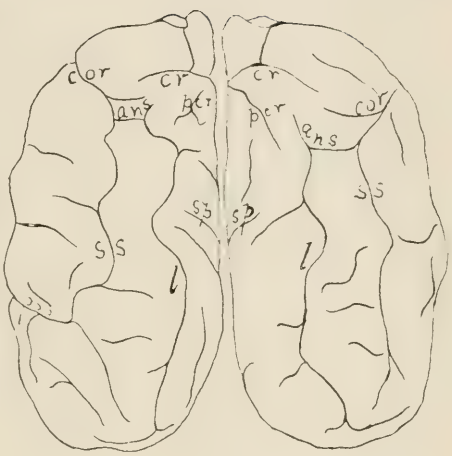




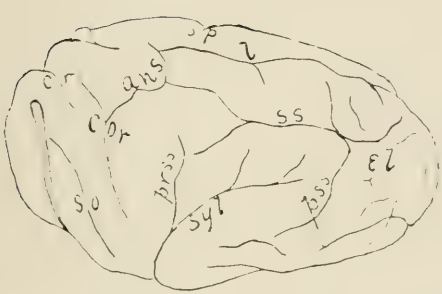




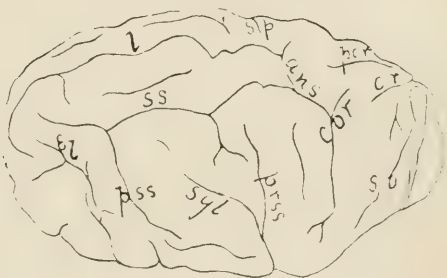
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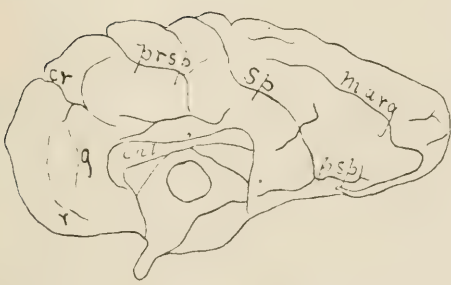
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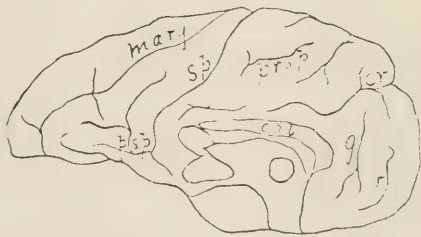
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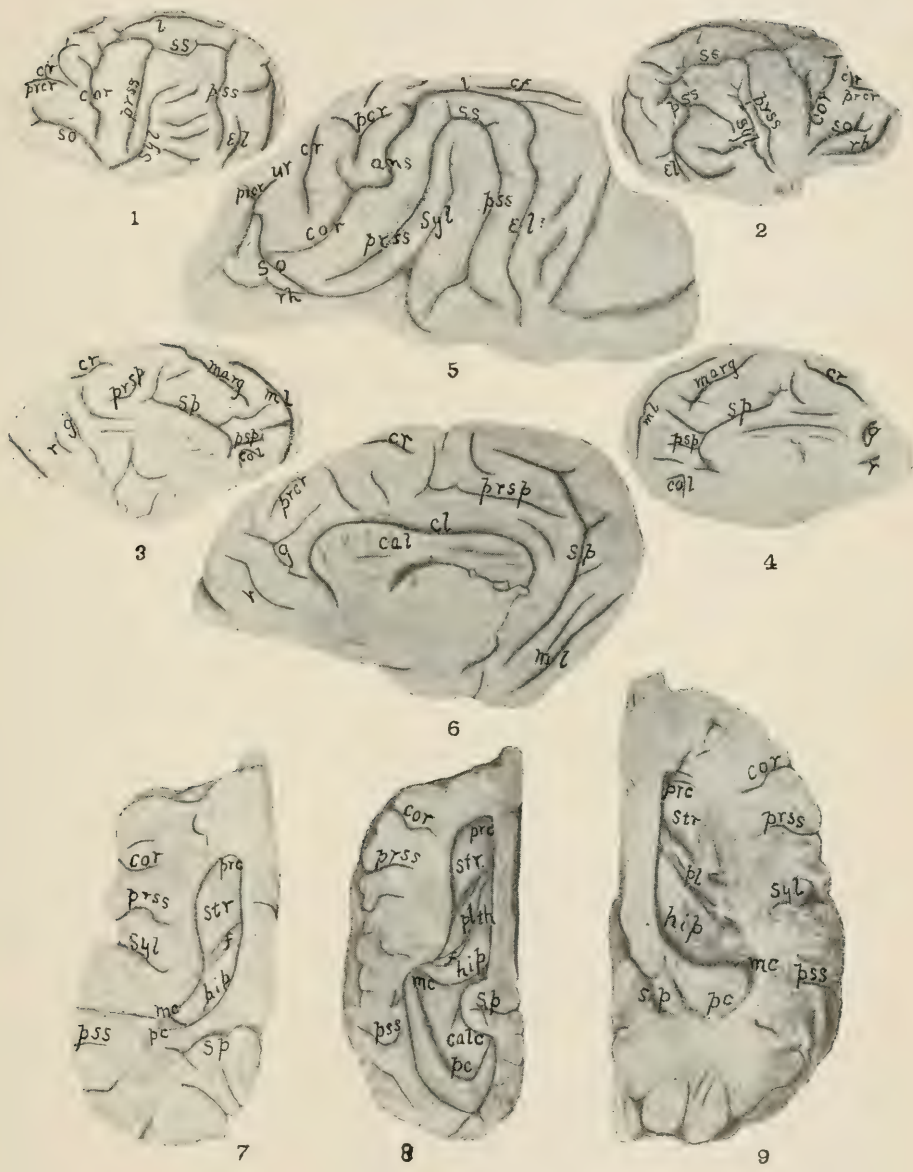
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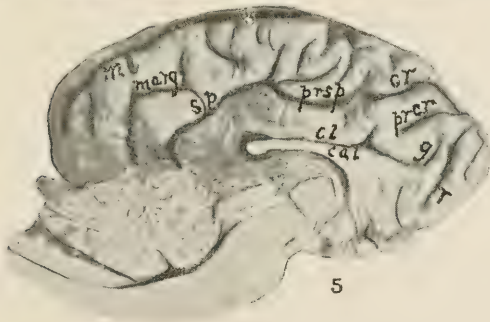
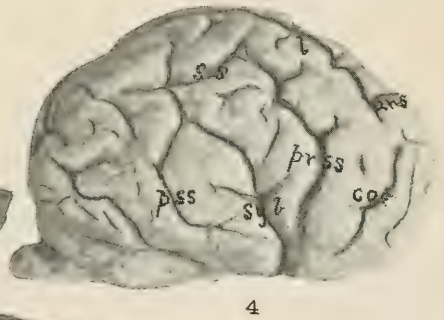
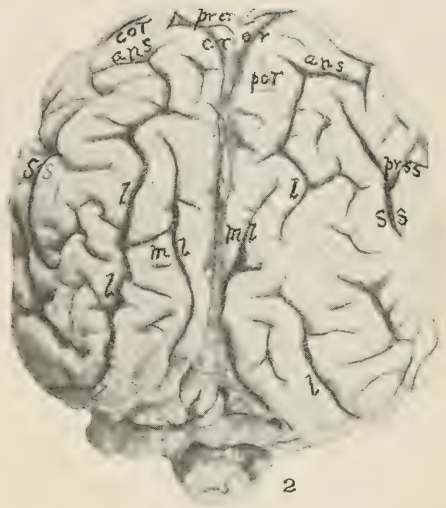
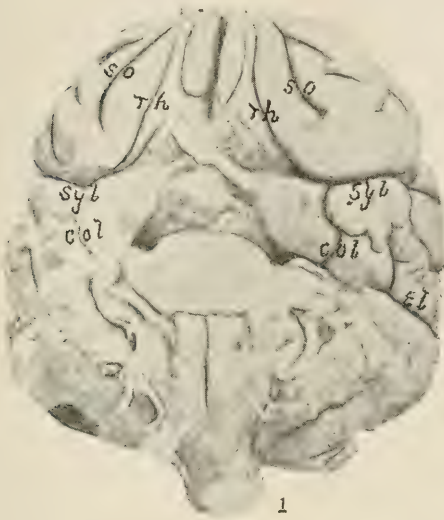
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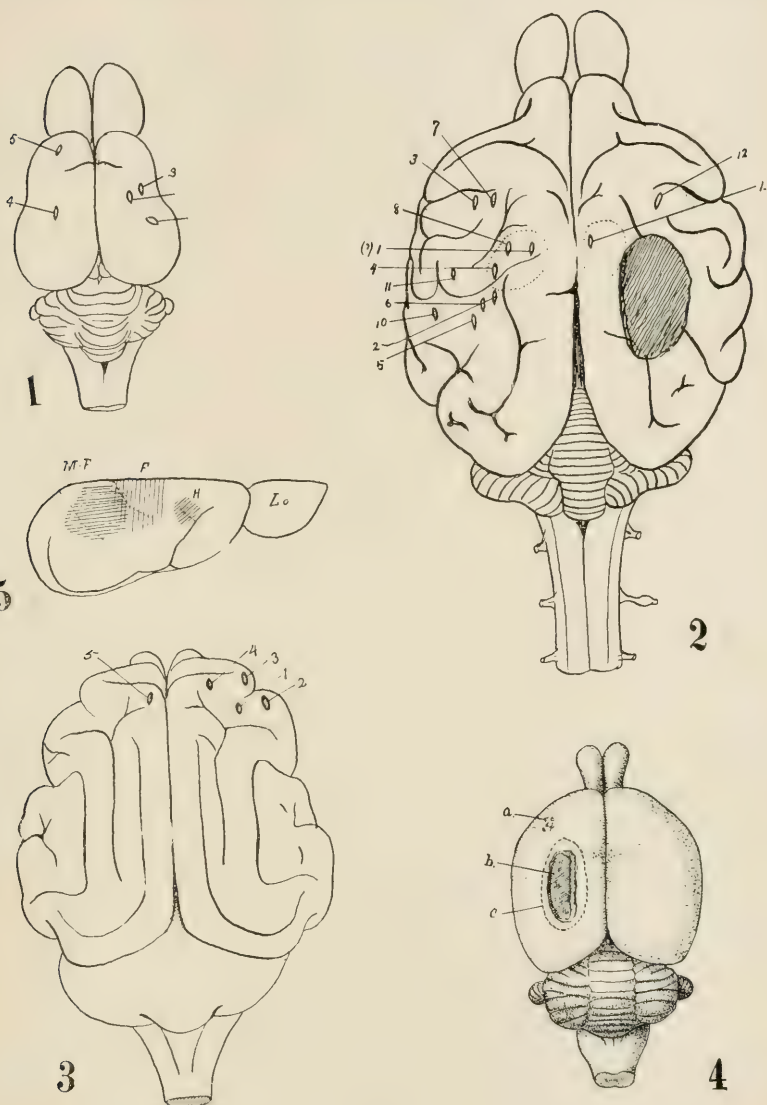














# CRITICAL REVIEW OF THE DATA AND GENERAL METHODS AND DEDUCTIONS OF MODERN NEUROLOGY.

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*Part I, With Plates XV to XIX.*

Neurological research seems to have struck a rich and important vein for progress in the shape of the 'neurone theory.' No less than a dozen pamphlets have during the last few years, proclaimed this new fertile standpoint. The old division of 'elements of the nervous system' into nerve-cells, nerve-fibers and neuroglia is replaced by a simpler one—nerve-elements (neurones) and neuroglia elements. A nerve-element, or neurone, consists of a cell body with nucleus and protoplasm and processes, either of the character of the protoplasm—dendrite, or of the character of a nerve-fiber—neurite. Nerve-fibers do not exist by themselves; a fiber is always a part of a cell only, a process of a nerve-cell. Moreover, it is considered to be an established fact that a fiber splits up into thin branches on its course and that the 'collaterals' and 'arborizations' terminate blindly without forming anastomoses with other cells.

Like all progress of science, this new conception, called neurone-theory, came to light in connection with a whole series of new observations, in neurogenesis and neurohistology. We shall see that it was slowly accepted in medicine, that it received various definitions and that it is in reality almost as if it meant simply the 'modern views of the nervous system.'

Just now it seems as if a careful review of the fundamental data and problems would hardly be out of place. Dogmatizing without adequate basis has led to discrediting the 'neurone-theory'; certain facts seemed to militate seriously against its current



presentation ; it is easy to see that much ' modern neurology ' is merely old concepts in new words and that the best advantages of modern neurology are missed by those who think that the neurone-theory pure and simple will bring the much needed salvation. Many important facts are forgotten over the generalizations drawn from them. His and Forel are hardly read by those initiated in the necessary generalizations from their publication and their eminently sound methods of work are pushed into the shadow by the schematic silhouette work.

The following sketches partly review certain facts not usually considered in the already numerous reviews on the ' neurone-theory,' partly they outline a standpoint suggested by data similar to those which led to the neurone-theory, a point of view from which the study of the nervous system receives a certain order, without persistently ignoring the valuable lessons which His and Forel have given. The replacing of Meynert's time-honored plan of the brain by one more in harmony with modern views, especially those suggested by work in pathology of the nervous system, has proved very stimulating both for instruction and for a working-hypothesis ; and the methods of observation and of reasoning which it suggests may prove fruitful to others.

### The Historical Development of the Neurone-Theory.

In view of the number of accounts of the historical development of the neurone-theory, among which I mention Waldeyer's, Lenhossék's, in the English literature Schaefer's, and in our own Baker's, Minot's, and especially Barker's, we might limit ourselves to the enumeration of the principal facts which constitute the difference from earlier views and help to establish the new conception. It seems, however, well to consider certain sides of the history of the neurone-theory frequently overlooked ; and to give careful summaries of the publications in question ; after that we point out the objections which are raised against the current formulation of the theory.

As a typical statement of the views just before the neu-

rone-theory was advanced, we may quote the short summary of the text-book of physiology of Landois, edition of 1887.

"The nervous elements present two distinct forms: nerve-fibers, non-medullated or medullated, and nerve-cells of various forms and functions. An aggregation of nerve-cells constitutes a nerve-ganglion. The fibers represent a conducting apparatus and serve to place the central nervous organs in connection with peripheral end-organs. The nerve-cells, however, besides transmitting impulses, act as physiological centers for automatic and reflex movements, and also for the sensory, perceptive, trophic, and secretory functions." After a detailed description of the histology of the nerve-fibers, the writer says concerning the *development* of nerve-fibers: "At first nerve-fibers consist only of fibrils, i. e. of axis-cylinders, which become covered with connective substance, and ultimately the white substance of Schwann is developed in some of them. The growth of the fibers takes place by elongation of the individual interannular segments, and also by the new formation of these." No hint is given of the origin of all the fibers from nerve-cells. "The ganglionic or nerve-cells have partly been considered as cells, partly as more complicated structures. We distinguish multipolar and bipolar nerve-cells, nerve-cells with connective tissue capsule and ganglionic cells with spiral fibers. The large cells of the spinal cord have among their processes one non-ramified 'axis-cylinder process' which becomes the axis-cylinder of a medullated nerve-fiber. Whether the cerebral nerve-cells have such processes is still doubtful, etc."

This statement is repeated in the later editions. The American one of 1892 gives merely a few editorial remarks in parentheses, to the effect that 'His and Forel claim that the protoplasmic processes do not anastomose but are merely in contact with one another,' and a statement that 'it is now certain that the cerebral cells too have processes.' It is very gratifying on the other hand, that W. T. Gowers, in the first edition of his "Manual of Diseases of the Nervous System," 1886, gives a view which has not received due attention in its day but was in many ways a perfect anticipation of the present

one, without sufficient generalization though, and without a full discussion of all available facts in its favor. The description of the pyramidal tract and its connection with the anterior horn cell is presented both in the text and in the drawing exactly as we would do today. He speaks of the pyramidal cell, its nerve-fiber and the terminal ramification of the latter in the spongy substance of the anterior horn, and of the anterior horn cell, the fiber proceeding from it, passing through the anterior root and nerve trunk to the muscle, where it divides and ramifies on the muscular fiber. This was written before August 1886, but that a nerve-fiber was *under all circumstances* merely a part of a cell, was not even accepted by Edinger,<sup>1</sup> who, as late as 1891, speaks of a double origin of nerve-fibers; first, from nerve-cells, as Deiters and others had shown for the connection of *motor* nerve-fibers and the large cells of motor nuclei and 'anterior horns,' and second, from the 'network consisting of all the processes of ganglion and glia-cells,' a mode of origin illustrated by Gerlach and others especially for the posterior root-fibers.

About August 1886, two Swiss scholars, Prof. His in Leipzig and Prof. Forel in Zürich, gave the medical public two studies which established the conception that the nervous system consists of independent cells like all the rest of the human organs. Prof. His stood on the ground of embryology, Prof. Forel used the results of the method of Golgi for an analysis of the experimental work with v. Gudden's method. The contribution of His<sup>2</sup> has undoubtedly furnished more direct data in favor of the new conception; and when Golgi, R. y Cajal, Kölliker, v. Lenhossék and others applied the silver method to embryonic material, a vast amount of detail sprang up enriching our knowledge so rapidly as to make it difficult to follow.

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<sup>1</sup> EDINGER, Structure of the Central Nervous System, Philadelphia, 1891, P. 42. See also illustrations and discussions in Gerlach, Stricker's Handbuch der Gewebelehre, Vol. 2, p. 679-685, 1872.

<sup>2</sup> HIS, W. Zur Geschichte des menschlichen Rückenmarkes und der Nerven wurzeln, 1886.

Prof. Forel's<sup>1</sup> classical study excels rather by the clearness and depth of critical analysis of a number of pathological and experimentally produced conditions and as such it is the most suggestive publication for any one who wishes to advance the anatomy of the nervous system on the ground of the study of pathological lesions and degenerations in man, notwithstanding its containing a number of minor errors.

Forel found the key to his problems in the discovery of Golgi. Before 1873, Camillo Golgi, a histologist and pathologist in Pavia, had discovered an extremely valuable method of impregnating nervous tissues with nitrate of silver. The great value of his procedure lies in the fact that his reagents do not affect *all* cells of a specimen, but only a few, and if an element is stained at all, it is so usually in its whole extent; the cell-body with all its processes and ramifications stands out in black. This peculiarity of the 'black stain,' the small number of cell-individuals brought out in their whole extent, furnished many unexpected data concerning the nerve-cells. About 1885 Golgi was 'discovered' by German histologists. Translations of a number of his contributions had appeared in this country long before that, in the 'Alienist and Neurologist,' but had not fallen on fertile ground. In Germany, too, reports of his work had been published, but were held in a very sober, hardly appreciative tone of scepticism. The exploitation of the points which could promote the general concepts came through Prof. Forel. Golgi's results are summarized by Forel as follows:

1. All the branches of the protoplasmic processes end blindly. They never anastomose, are uneven and show no fibrillary structure.
2. Every nerve-cell is *unipolar*, i. e. it has only one nerve process.
3. This nerve-process has very fine branches.
4. In the cells of the *first category* the nerve-process, after giving off a few fine collaterals, forms a medullated fiber;

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<sup>1</sup> FOREL, AUG. Einige Hirnanatomische Betrachtungen und Ergebnisse. Arch. f. Psych. XVIII.



in the cells of the *second category*, the nerve-process dissolves completely into fibrils before it becomes a real fiber. The cells of the first type are motor, those of the second type sensory, and the terminations of the *fibers* of both join in the *anastomoses* of a common network of fibrils.

This is, on the main, the first exact demonstration of the standpoint of *Gerlach* (apart from the denial of anastomoses of the dendrites), with a greater number of corrections of detail; but the delicacy of the new specimens suggested to Forel more than Gerlach's views. Forel's first criticism deals with the continuity of the net-work of fibrils. The absolute absence of actually visible anastomoses in the Golgi specimens is quite striking. Further it is difficult to conceive how these thin fibrils coming from different cells would grow together at their ends and how the growth of the individual cells in the years of development of the nervous system could go on if there were real continuity instead of free end-buds. The next step is the *assumption* that all the fiber-systems and 'net-works' of fibrils throughout the nervous system are nothing but nerve-processes of definite sets of nerve-cells, and further that Golgi is wrong in calling all the cells motor whose nerve-process becomes a long fiber. The excess of fibers in the nervous system is only apparent, not real; the fibers are so much longer and larger than the cell 'body' to which they belong that the preponderance of 'white matter' over 'gray matter' is not very surprising.

The evidence which Forel adduces for the radical conception that the nervous system consists of cells without anastomoses of the processes and not of independent fibers plus cells is taken from the inability of finding anastomoses in Golgi preparations, and from the results with the method of Gudden and 'secondary degenerations' generally. Since the latter are relatively little studied by the physicians on our side of the Ocean, notwithstanding the summary of Séguin (*Arch. of Med.* X, 1892) and Spitzka's work, I mention a few of the fundamental results which Forel discusses. The first one refers to the external geniculate body, the principal end-station of the optic nerves, and the place of origin of a great share of the 'optic

radiation.' In the external geniculate body, all the *cells* degenerate when the occipital lobe (with the optic radiation) is removed from the new-born ; if however, the eyes are removed, merely the '*gelatinous substance*' disappears, so that the cells become more closely crowded. Forel explains this as follows : the large cells of the retina send their fibers into the external geniculate body. There they lose the medullary sheath and split up in end-brushes, or end-arborizations, merely coming into contact with the cells and their processes, and helping to constitute the '*gelatinous substance*.' The gelatinous substance is not homogenous, but consists (besides the neuroglia and blood-vessels) of these end-brushes and the protoplasmic processes of the cells. When the cells in the eye are removed by operation, their processes degenerate and are resorbed, and consequently the cells in the external geniculate body come more closely together. If, however, the cortex is removed, the cells of the external geniculate body are affected and degenerate, because their end-brushes are cut off without a chance of regeneration ; the gelatinous substance, as far as the terminal fibers of the optic nerve constitute it, is not directly affected ; only the *cells* of the external geniculate body and their processes decay and are obliterated. If the condition is produced in an adult animal, or by pathological conditions in the adult man, the '*retrograde degeneration*,' i. e. the affection of the cells which are merely cut through at the termination of their fibers, is not so marked, and as we know now through experiments with Nissl's method, a more or less transitory matter. (For a similar illustration published 1891, see the chapter on '*motor neurones*.')

Another interesting fact is demonstrated with regard to the peripheral motor nerve-elements. v. Gudden showed that tearing out a facial nerve from the Fallopian canal in the new-born leads to complete degeneration, not only of the remaining peripheral branches to the muscles as Waller had thought but also of the cells of the facial nucleus and the remaining '*central stump*'; the degeneration of the cells and central stump does not take place, however, when the tear or section occurs further in the periphery and a chance at regener-

ation presents itself. In this case the axis-cylinders of the central stump grow out again towards the muscles to which they belong, if, at least, they can follow a bed along which to grow, especially after nerve-suture. The study of Forel contains a number of considerations on the slight differences between what is seen in the animal when operated young or old, and also between various findings in man, and, further, illustrations of the problems in the anatomy of the fillet (retrograde atrophy and retrograde degeneration), of the auditory centers, trigeminus and pyramidal tract.

The *problem of experimental anatomy* of the brain might be formulated as we have it now on ground of this early study of Forel. He did not summarize it in the following words but has all the material expressed in the various parts of the paper :

1. All nerve-fibers are merely processes of cells. They terminate blindly in end-brushes, like the protoplasmic processes without anastomoses. The interrelation of the nerve-elements takes place *by contact, not by the continuity of a network*. The net-work of Gerlach is a false net-work [comparable not with a net, but with the appearance of a dense forest where each twig belongs to only one tree, although it may be difficult on a photograph to trace each correctly].

2. To call the cell body the trophic center of a nerve-fiber is justified only in the sense that the nerve-fiber is a part of the entire cell and that it is subject to the general laws of cell-vitality. (Any part of the cell which is cut off from the nucleus will degenerate).

3. The results of experimental anatomy and the so-called secondary and tertiary degenerations are satisfactorily explained on this basis ; further, a discussion of secondary degenerations etc. is only complete when the questions are put with these facts in view. We should not merely study fiber-tracts but always search for the cell-bodies to which the fibers belong.

Forel does not summarize all the conclusions, since his aim is rather the explanation of certain disputed facts relating to von Gudden's atrophy method. In a later publication he furnishes

splendid illustrations of the principal points just set forth. We shall refer to them in full.

Wilhelm His arrived at similar conclusions on ground of embryological observations and considerations. I mention here a summary of propositions which the famous embryologist communicated to the Anat. Gesellschaft.<sup>1</sup>

1. There is a period in the embryonic life in which no nerve fibers exist, neither central nor peripheral ones.

2. The motor nerves originate as processes of definite cells of the spinal cord and brain.

3. The axis-cylinder processes appear as the first processes of the motor cells; the ramified (protoplasmic) processes are formed considerably later.

4. The motor cells show early a fibrillary cell-body and the fibrillation is continued into the relatively broad axis-cylinder.

5. The motor cells, both of the spinal cord and brain are located in definite and constant zones of the medullary tube (brain-axis and spinal cord). The latter consist of a floor-plate and roof-plate which connect the lateral walls in the median line. The lateral wall again is divided into a dorso-lateral (alar) and a ventro-lateral (basal) part.

6. All motor nerve-roots originate from cells of the ventro-lateral (basal) part of the tube; but not all the cells of that part send their axis-cylinder into the motor roots. A few of them grow towards the anterior commissure and others seem to enter into the formation of the longitudinal tracts of the cord and brain.

7. The motor nerve-fibers leave the tube in several types (See the copy of the drawing of His, Fig. 4): A. The type of the motor spinal roots and of the 12th, 6th and 3rd cranial nerves. B. The type of the spinal accessory and the motor divisions of the pneumogastric, glossopharyngeal and 5th.—origin from a lateral nucleus of the 'basal plate' and exit at the

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<sup>1</sup>Herr Wilhelm His, Ueber die embryonale Entwicklung des Nervenbahnen. Anat. Anzeiger, Vol. III, p. 449-505.



junction of dorso-lateral and ventro-lateral lamina. C. Type of the facial nerve—it originates from a lateral cell-nest of the basal plate; runs towards the median line, then turns through a 'knee' around the median cell-nest (abducens group) and outward between the dorso-lateral and the ventro-lateral part of the lateral wall of the medulla. D. The type of the fourth nerve—the cell-nest lies in the basal lamina; from there the fibers grow outward, into the roof of the tube and after decussating with the bundle from the opposite side, come to the surface.

8. The cells of the spinal ganglion have at first no long processes; then follows a stage when every cell is bipolar, and later on, the spinal ganglion cell is characterized by the presence of two fibrillary axis-cylinder-processes which leave the cell in opposite directions and to which the cell-body takes an eccentric position. The central processes of the spinal cells grow towards the medullary tube and remain to a great extent on its surface, forming a longitudinal tract.

9. In the spinal cord the ingrowing sensory roots form the primary posterior column; within the 'brain' the so-called 'ascending roots', the roots of the pneumogastric, glosso-pharyngeal, nerve of Wrisberg and the fifth are, as it were, the posterior column-formation of the medulla.

10. Not all the sensory root fibers of the neural tube grow simultaneously. At first there are fewer fibers than later. This holds also for the central tracts, the anterior commissures and the antero-lateral columns.

11. The 'ascending roots' are first quite short and grow successively longer.

12. The peripheral nerve-trunks too grow gradually.

In the above studies we have the root and the soul of the neurone-theory. It is, however, nothing but fair to say that Ramón y Cajal, the greatest promotor of neurology that Spain ever has produced, should be mentioned as the chief confirmer of the same concept. This is certain that none has discovered and demonstrated more individual details in confirmation of the views of Forel and His than this indefatigable Madrid histologist, and as he says himself, he has done what neither His nor

Forel have done conclusively ; he demonstrates the blind arborizations or end-brushes of so many kinds of nerve-fibers and the connection of the latter with cell-bodies in the cerebellum, the medulla, olfactory bulb, retina, optic centers, the great sympathetic, the cerebral cortex, that the concept and the detailed data are established beyond doubt (sin sombra alguna de duda<sup>1</sup>).

The principal generalizations which we can derive from Cajal are as follows :

1. There is no substantial continuity between the processes of different nerve-cells. The nerve-elements represent cell-units, for which he accepts Waldeyer's term 'neurone'.

2. While Golgi assumed that the protoplasmic processes of nerve-cells had a purely nutritive function, Ramón y Cajal renders it probable that the protoplasmic processes are those parts of a neurone with which the arborizations of other neurones come most likely into contact and that the contact with the cell-body itself is exceptional, being found only in those cells in which there are no protoplasmic processes (spinal ganglion, retina).

3. The spreading of impulses received is cellulipetal in the protoplasmic processes and centrifugal in the axis-cylinder (law of dynamic polarization).

We must mention here that one of Golgi's chief discoveries is the demonstration of fibrils or collaterals which branch at right angles from the nerve-process of almost every cell soon after its origin. The conception of Deiters, that the nerve-process was characterized by having no branches before its final termination, was modified by Golgi, inasmuch as he found that not only the protoplasmic processes have branches but also the nerve-process ; the difference lies in the branching at acute angles in the case of the dendrite, and at right angles in the case of the collaterals ; further, it is easy to see that the dendrites *taper* towards the periphery, whereas the collaterals are smooth and

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<sup>1</sup>Dr. D. Santiago Ramón y Cajal, Nuevo concepto de la Histología de los Centros Nerviosos, Barcelona, 1893.

even, diminishing in calibre only by splitting up into terminal brushes and ending in little nodules. Golgi had also observed that the protoplasmic processes chiefly terminated near the blood-vessels and had therefore largely a trophic function, a view strongly opposed by others. For the transmission of nerve-impulses, according to Golgi, the collaterals are sufficient; the cell-body with the protoplasmic processes stands above the neural circuit as the trophic focus of the nerve element. This same view is maintained by *Nansen* on the ground of studies on invertebrates. The reader will see at a glance what the three investigators give when looking at the two figures (Fig. 1, Plate XV)—A. representing the view of *Golgi* and of *Nansen* (from *Nansen's* work 1887), B. the view of *van Gehuchten-Cajal* (from the latter's *nuevo Concepto*, etc). In a later chapter we shall have to speak of the views of *Berkeley* and *Held*.

This short sketch may suffice for the history of the question before us, the development of the neurone-theory and of the embryological and experimental method. While the neurone-concept was slowly accepted by the almost totality of the investigators who become acquainted with it, there remained a few opponents, open or disguised. It will be desirable to pass them in review.

The strongest and most emphatic opposition comes from *Golgi* and his pupils. As the publication of Dr. *Achille Monti*<sup>1</sup> is probably not accessible to most of the readers of these notes, an abstract is given here.

*Golgi* had published in 1875 a description of the olfactory bulbs of mammals which established the following facts: The fibers of the olfactory nerve enter the olfactory glomeruli, ramify repeatedly at right angles, and form an intimate meshwork. A further constituent of the glomeruli are the dendrites (protoplasmic processes) of the large and small cells of the *bulb*, and finally also *collaterals and nerve fibers from the olfactory tract*. These results are reproduced from the original in the second

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<sup>1</sup> Sulla fina anatomia del bulbo olfattorio. Fatti vecchi e nuovi che contraddicono alla teoria dei neuroni. Nota del Dott. *Achille Monti*. Pavia; 1895.

plate of the atlas of Golgi, published by Fischer in Jena, in 1894. Fifteen years later Ramón y Cajal published a remarkably simple sketch of the architecture of the same region, and since then v. Gehuchten and Martin<sup>1</sup>, Pedro Ramón<sup>2</sup>, Kölliker<sup>3</sup>, Retzius<sup>4</sup>, Calleja<sup>5</sup>, and Conil<sup>6</sup>, have essentially corroborated it; it has passed into almost all of the later text books. It establishes only the following connections:

1. The olfactory nerve fibers terminate blindly within the olfactory glomeruli. There they come into contact with 2. the dendrites of the large "mitral cells" whose fiber processes help to constitute the olfactory tract. *The termination in the glomeruli of fibers from the olfactory tract is strongly denied by all these writers*, and the whole arrangement is commonly used as a paradigm of the connection of peripheral and central afferent neurones, and also as absolute evidence for the 'law of dynamic polarization,' according to which the dendrites receive the nerve impulses and they pass through them into the nerve fibers. Monti reestablishes completely the *older* observations of Golgi (especially the presence of recurrent fibers to the glomeruli) and demonstrates a certain superficiality of the investigators mentioned. He points out that their inaccurate descriptions do not furnish an unassailable basis both for the theory of the conductive function of the dendrites and even for the mere contact connection between nerve elements since the network in the glomeruli is too complex and recurrent collaterals are undeniably present.

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<sup>1</sup> Van Gehuchten et Martin: Le bulbe olfactif chez quelques mammifères. La Cellule, T. VII, fasc. II.

<sup>2</sup> Pedro Ramón: Estructura de los bulbos olfactorios de las aves; Gaceta sanit. de Barcelona; Julio, 1890; and

El encephalo de los reptiles; III, Bulbo olfactorio, Septiembre, 1891.

<sup>3</sup> Kölliker: Ueber den feineren Bau des Bulbus olfactorius; Würzburger physikalisch.-Med. Gesellschaft; Dec. 1891.

<sup>4</sup> Retzius: Die Endigungsweise der Riechnerven. Biologische Untersuchungen, Neue Folge, III, 3, 1892.

<sup>5</sup> Calleja: La region olfactoria del cerebro; Tesi di Madrid, 1894.

<sup>6</sup> Conil: Mémoires de la Société de Biologie, 1892, p. 179.



It is somewhat difficult to see why the omissions of the writers succeeding Golgi, even when conceded, should furnish so much evidence *against* the general trend of their explanations. Monti and Golgi undoubtedly demonstrate by their work a spirit of great accuracy and conservatism, but it appears almost as if it were sufficient to state the case as a warning against too hasty and schematic generalizations rather than as proof for a strict negation of the newer working hypotheses. Van Gehuchten and Cajal must look for more evidence, it is true, to make an undeniable law out of their hypothesis; in this we agree with Monti.

Golgi's chief objection rests on his interpretation of the character of the diffuse network of the end fibrils. He claims that his opponents have not the true scientific spirit of accuracy when they consider the question settled in favor of the forest simile with an absolute denial of anastomoses. He himself stops before the inextricable maze and leaves the question undecided. He favors the presence of a real network but does not deny Forel's and Cajal's views absolutely, as his opponents do the view of the network with anastomosis.

Another objection is raised by Dogiel who maintains the presence of anastomoses in the cells of the retina. The overwhelming denial by other investigators of the retina would, however, invalidate his evidence considerably.

As a very serious objection we mention the ever recurring description of regenerating fibers in the cut-off end of a nerve, before the central nerve processes have reached the portion peripheral to the cut. *Bowlby*<sup>1</sup>, and again *Kennedy*<sup>2</sup>, claim to have seen new nerve fibers formed within the peripheral stump, not coming from the central stump, and *later* growing together with the fibers of the central stump. This would imply the growth of nerve fibers from something else than nerve cells and the possibility would hit fatally the dogma that no nerve fiber

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<sup>1</sup> Bowlby: *Injuries and diseases of nerves*; London, 1889.

<sup>2</sup> Kennedy: On the regeneration of nerves. *Proceedings of the Royal Society*, March 11, 1897.

can exist except as a process of a nerve cell. All this is emphatically denied by all writers outside of England. Prof. C. Huber, of Michigan University, who has studied the question with Prof. Howell, and to whom a similar statement had been ascribed, writes me that he has seen no evidence in favor of such assumptions. In connection with this we must mention a discussion which was carried on in the camp of morphologists, and which is never referred to in the discussions concerning the neurone theory. The most important contribution is undoubtedly one of J. Beard, the histogenesis of nerve<sup>1</sup>. A. Dohrn, the head of the Zoological Station at Naples, published memoirs on this subject which fully supported Beard's own way of seeing things. Dohrn (quoted in Beard's article) says:

"Thus we have the picture of a nerve such as is found typically everywhere. The nuclei are Schwann's nuclei, the light shining cylinders are the axis cylinders, the plasma is the soil of Schwann's and of the medullary sheath appearing later. These four elements constituting the typical nerve, are exclusively products of ectoderm cells disposed in chains for the formation of individual fibers." Beard says (p, 295): "These chains (i. e. their nuclei) proceed to secrete, from before backwards as fast as they are formed, nerve fibrils or axis cylinders outside of themselves, and each linear row secretes one axis cylinder." In the case of the motor nerves "the chains of cells leave the cord in a manner often described, and finally detailed by Dohrn in more than one publication. The blunted peripheral termination of the chain becomes applied to the muscle plate, and, with great certainty I can repeat what I have more than once stated, that the terminal end-plates of muscle and of the electric organs are formed from the wandering of such cells along with the nerve-forming cells *sensu stricto* from the anterior horn to the terminal region. *These terminal cells must be regarded as ganglionic in character.* In connection with these chains of cells the formation of nerve takes place just as described in the above." He further draws attention to the

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<sup>1</sup> Anatomischer Anzeiger, VII, pp. 290-302.

views of Vignal who considers the nuclei of Ranvier's nodes as mesoblastic, but shows that they are concerned in the lengthening of the nerve, and that to this end they give origin to intercalary segments.

*Dohrn* himself (*Anatomischer Anzeiger*, VII, pp. 348-351) practically defeated *Beard's* view by stating that he is now convinced of the *terminal* growth of the axis cylinder in the sense of *His*; and that the cells of *Schwann's* sheath were mesoblastic; that he had seen fibrils develop independently beyond the "chain of cells;" which would corroborate the neurone theory. *Beard*, as far as I am aware, has not given up his heterodox view as *Dohrn* did; I give it therefore a place in this summary as a possible, though not probable, objection to the neurone theory.

*Held's* recent finding concerning the concrescence of nerve fiber terminations and cells (instead of simple contact) is a very vital objection to certain hasty conceptions of the neurone theory. The facts observed by him are the following: In the new born dog there is in the trapezoid nucleus a distinct limiting line where the end-brushes of a neurite and the protoplasmic body of the cell meet, such as we find wherever two different substances come into contact with each other. In the dog nine days old, however, this limiting line has disappeared and it is impossible to make out a boundary between the end-brushes of the other cell and the cell protoplasm itself. This speaks very strongly in favor of actual concrescence and not mere contact. It is evident that the *growth* of the cell processes becomes by no means more intricate on ground of this observation. The branches divide and those which find definite connection with other cells become fixed, the others remain free. The review in the *Zeitschrift für Hynotismus* says nothing of other anastomoses [see however our own summary in a later part of other discussions]. Fundamental principles, especially the axiom of the cellular theory, are just as easily understood if we have to admit this observation, as a fact. The fatal blow hits merely the hypothesis of the contractility of the nerve elements which has been exploited for the explanation of sleep and kindred

conditions by Duval, on ground of the considerations of Rabl-Rückhard and Weidersheim, who suggested the contractility of nerve elements by means of which one cell can withdraw from contact with another; or by Ramón y Cajal who attributed to the neuroglia an active rôle in the production of sleep and rest. In these conditions the neuroglia would separate the cells from one another while, during activity, it would withdraw and make contact possible. For the time being, these are reveries which have been pleasantly or unpleasantly interrupted by Held. They have really nothing to do with the fundamental concepts of the neurone theory and will not occupy us any longer here.

We might however, look for danger in another quarter, namely in the recent development of our knowledge of neuroglia, as presented by *Weigert* in his *Beiträge zur Kenntnis der normalen menschlichen Neuroglia*, 1895. All the evidence of histogenesis goes to prove that the neuroglia elements are of ectodermal origin, and are derived from the same cells as the nerve cells<sup>1</sup>. For a long time views identical with the general principles of the neurone theory have been held with regard to the neuroglia, even before the neurone theory existed, and by men who deny its justification, such as Golgi. They (Fromann, Golgi and others) claimed that the neuroglia consists only of cells and their processes. Weigert admits this only for the embryonic condition. "In the full grown state the neuroglia consists of cells and *moreover* of fibers, and the latter preponderate in such enormous proportion with regard to the space taken up by them that they are to be considered the more important part of the 'neuroglia.' These fibers are by no means processes of cells, but fibers which are perfectly differentiated from the protoplasm."

We witness in this a peculiar difference in the development of the fundamental conceptions concerning two sister structures. The neuroglia having conquered a position in the

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<sup>1</sup> See Alfred Schaper: Die frühesten Differenzierungs-vorgänge im Central nervensystems. Archiv für Entwicklungsmechanik der Organismen V, pp. 81-232.



cellular hypothesis not only regarding its origin but its persistent existence, is described as being cellular in its origin but consisting largely of fibers independent of cells in its later stages. The neurones, or nervous substance in the narrower sense of the word, used to be looked upon as a mass of fibers, a few (the peripheral motor fibers at least) in distinct connection with the cells from which they grow, others originating from the network of the spongy substance and only indicating connection with cells and masses of cells. Now we wish to establish for the nerve elements just that view which was held for the neuroglia, and which was dethroned by Weigert. We tried this notwithstanding certain difficulties concerning the monocellular character of the peripheral nerve-fibers. The peripheral nerve-fibers consist after all of more than one cell, unless we have it strictly understood that the cell-unit consists only of the nerve cell-body, dendrites and axis-cylinder process, and that the sheath and its nuclei are an additional coat, not really belonging to the cell-unit, but formed by epiphytes. If we follow Vignal and Ranvier, we assume that the myelin sheath and the nuclei of the inter-nodes have nothing to do with the neurone itself, but are mesoblastic epiphytes. If, however, we follow other observers who consider the myelin sheath a product of the axis-cylinder, the difficulty with the 'epiphytes' would be shifted; especially the effect of secondary degeneration on the myelin would be free of serious contradiction with the neurone-concept as a 'one-cell-concept.' However this be, we should make the mental reservation, when speaking of a motor cell-unit or neurone, that we do not include the nuclei of the internodes, i. e. do not speak of all that is usually included in the description of a 'fiber;' further, that there still is some uncertainty as to whether the myelin belongs to the neurone or the epiphytes.

There are two points to be mentioned that will relieve our fears of the analogy with the fate of the neuroglia. The first one lies in the nature of Weigert's arguments. According to him the neuroglia is a real intercellular substance, i. e. 'non-nervous material belonging to the group of modified cell-sub-

stances which are emancipated from the cell bodies and which no longer can be considered to be immediately connected with the cell.' "1. Because with Weigert's new stain everything nervous and even the protoplasm of the neuroglia cells, remains unstained, the fibers of the neuroglia however are stained dark blue (conclusion per exclusionem).

2. Because the fibers contain a modified substance which is no longer protoplasmic, but emancipated from the cell body.

3. Because the fibers (and the cells belonging to them) react under pathological conditions just as connective tissue, i. e., they proliferate when the specific nervous tissue perishes" (pp. 115-117).

The clause in the third reason seems significant. It relates to the fact that the cells too proliferate [and must proliferate in order to produce fibrils]. Further the reason for the complete emancipation of the fibrils is decidedly not *absolutely* convincing. The writer could never resist a certain comparison of the results of Weigert's neuroglia stain with the results of his stain for medullated fibers. Only those parts of the neurone retain the hæmatoxylin which have enough myelin and kindred substances, namely, in a correct stain, only the medullated part of the fiber. Yet we have reason to consider the myelin sheath a part of the neurone notwithstanding its peculiarity of chemical constitution. The neuroglia stain does not give a complete stain of the neuroglia either, but only of the parts which contain a definite substance. The difference lies in the greater number of the fibrils, the lesser degree of organization, and the difference in the distribution of this kind of specially stainable substance which is by no means of a known constitution as in the case of the myelin. Weigert advances "with the greatest safety" the following theses (p. 105):

1. The neuroglia fibers which, so far, have been taken for processes of the Deiters' cells, are not structures identical with the protoplasm, but an absolutely different substance.

2. The chemical difference does not appear slowly at a more or less long distance from the cell-body in the "process-

es," but the differentiation exists from the beginning, in the immediate neighborhood of the nucleus itself.

3. Most of the so-called processes of the cells are no "processes," because two of them form one thread passing by the cell without in any way being interrupted by the cell body, as would be the case with "processes" taking their origin in the cell bodies. *We are not dealing with processes of cells but with fibers which are completely differentiated from the protoplasm.* They may have been processes in the embryonic period only.

This somewhat dogmatic view does not appear absolutely convincing, since the "*loops*" *are not within the contour of the cell-body but form the outline*, and many of them are outside the outline and probably belong to other cells. Weigert's view would seem to be the only possible one if in cells like those of his Fig. 1, Plate I, points of cross sections of fibrils could be seen inside of the outline, such as I have never been able to find either in sections kindly presented to me by Prof. Weigert, or in my own preparations made with his method.

We are not absolutely convinced of the obsolescence of the cell-idea in the neuroglia, even of the adult; and if we should become convinced of it by more strengthening evidence,<sup>1</sup> we might console ourselves with the 'intercellular' connective tissue nature of this inferior substance.

Yet, that which was thus anticipated has since been realized by S. Apathy,<sup>2</sup> who sees the unit of conduction in fibrils (as Gowers does in his Dynamics of Life) passing through several cells; between fibrils among themselves and also between cells he sees anastomoses—the completest revolution of the

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<sup>1</sup>F. Reinke (über die Neuroglia in der weissen Substanz des Rückenmarkes vom erwachsenen Menschen. Arch. f. mikr. Anat, Vol. L, 1897) corroborates Weigert, saying that he has seen the true protoplasmic processes of neuroglia cells, but also the absolutely different and *independent* fibrils of Weigert. If this is true, we should of course have to bow to the evidence given.

<sup>2</sup>Das leitende Element des Nervensystems und seine topographischen Beziehungen zu den zellar. Erste Mittheilung. Mitth. aus der zoolog. Station zu Neapel, 1897.

views of the day, but only 'demonstrated' fully in invertebrates, evidence only being 'promised' for the vertebrates. The demonstration of the preparations in Wood's Hole has convinced most men of the correctness of his claim as regards the existence of fibrils, but not quite that of the claim that these fibrils pass from one 'neurone' into another. If we consider further that Lugaro and especially Becker and Bethe have better evidence than ever before of the existence of fibrils in human nerve-cells, we must admit that the problem of the nerve-unit is a greater puzzle now than two years ago when the dogma of the 'neurone' was almost looked upon as a finality.

This short historical sketch must suffice for the present introduction and cannot help leaving the impression that the dogmatic inclinations have played a certain trick on those who believe the definition of the 'neurone' on the first page to be a perfect soother of all suspicion and skepticism concerning the units. We have certain embryological facts which we owe to His; we have some experience concerning the life of the 'neurone' under the influence of injuries, the explanation of which we owe to Forel; we have the charming schematic pictures of the Golgi preparations in the hands of Golgi, Cajal and others: much evidence goes in favor of the monocellular character of the 'neurone', so that we may justly call the neurone-theory the cell-theory, although even in a simple portion such as the peripheral fiber we stand before a puzzling symbiosis of many cells. Its formation in the period of development has been submitted to a fruitful study by Wlassak, but for an understanding of all the conditions difficulties increase in the fully developed state, and the clean lines of the individual cells become less plain. We come across uncertainties along the lines of the symbiosis noticed in the medullated fibres, and, concerning the cells, doubt is now thrown on the real value of the Golgi pictures which are not capable of producing all the fibrils discovered lately and which therefore would not show anastomoses of fibrils, even if they existed.

Before wading into the deep water of details, we return to some important data of His and Forel and others, and try to



get an orientation of the heavy lines of architecture of the apparatus under study, making use of the solid data, but not expressing any opinion yet on the details of interrelation between the 'neurones.' We assume as a working hypothesis that the 'neurones' are units such as His and Forel and also Cajal describe them, but avoid any assumptions which would necessarily collide with any of the difficulties just reviewed.

### Outline of an Architecture of the Nervous System.

In order not to move in abstract realms, we give in the following pages a short outline of the general architecture of the nervous system. We shall then be able to refer to concrete conditions in such a manner as to avoid misunderstanding. We must necessarily take some position in the general method from which to approach neurology, and we choose the one of evolution in this sense that we take the phylogenetically oldest mechanisms as the starting point instead of proceeding from the cortex through the 'projection-systems' after Meynert's fashion.

We are inclined to start in a consideration of the nervous system from an assumed unit, the brain, and to look upon the peripheral nerves as its afferent and efferent wires. This method has great disadvantages. It starts out with what is least known and most complicated and creates an ego-centric view of the human mechanism which stands in the way of an understanding of many of the most useful facts acquired by neurology. In building up the following sketch, we begin at the foundation, and proceed towards the most differentiated mechanisms after having established the ground upon which to build them.

We start from a sketch of the nervous system of a worm. The rain-worm is a distinctly segmented animal, bilaterally symmetrical, as the vertebrates. Its nervous system consists of a head-ganglion above the oral opening, a strand on each side of the oesophagus extending from it to the first ganglion of the ventral ganglion-chains and forming what the Germans call the 'Schlundring', and the ventral ganglion-chain formed of a ven-

tral ganglion for each inner segment and longitudinal connecting strands between the ganglia. The structure of these ganglia is illustrated by the following elements:

Specialized 'sensory' cells among the epithelia of the skin send fiber processes into the ganglion where they dissolve in an arborization, coming into contact with the branches of the cells which are connected by a process with the muscles located under the epidermis; and further cells, the processes of which merely connect various parts of one ganglion or of several ganglia together.

This gives us the following three types of elements:

1. Afferent elements, specialized epithelia, which send a fiber-process into a ganglion where it ramifies into branches ending in contact with many cells; one or more of the branches may even join the longitudinal strand and terminate near the cells of neighboring ganglion. The fundamental point is that one spot in the sensory surface (skin) becomes connected with *many* cells.<sup>1</sup>

2. Shunt cells or intermediate elements, cells which merely connect various parts of one or more ganglia. Their processes do not leave the 'central nervous system.'

3. The motor nerve-elements, called 'motor' because they are in definite connection with the muscles. The cell body forms part of the ganglion, its fiber a part of the 'peripheral nerve', and the termination corresponds to the muscular end-plate.

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<sup>1</sup>The afferent elements are usually called sensory; this term is however greatly misleading. If sensory is to mean 'the bearer of sensation,' it is wrong; for the sensation lies not in these elements, but in a mechanism or combination of many cells. If the cord is severed in a vertebrate, the afferent fibers 'below' the lesion remain afferent, as the presence of reflexes shows; but they are in no manner sensory, bearers of sensation. It is the custom of carrying incompletely digested or obsolete psychological terms into physiology which leads us to this laxity of terminology. In the future study we shall rather avoid the word sensory as an anatomical attribute and reserve it to psychophysical processes except perhaps where stylistic reasons seem to demand leniency in the choice of synonyms. The term 'afferent' is as a rule more correct and preferable, because it says just what is meant and suggests no false psychical inferences.

Passing over to the vertebrates, we start from a stage of development of the chick such as represented in the figures 10-13 in Dejerine's anatomy taken from Duval's atlas. The dorsal lamina of the embryo shows a longitudinal groove which tends to close itself. In Dejerine's Fig. 12 we see the neural tube almost closed. Along the dorsal suture of the tube special clusters of cells are noticeable on either side which later are known as 'sensory' ganglia. *His* called the formation 'neural ridge' and we thus start with the 'neural tube' and the 'neural ridges' on either side of the tube. Comparative neurology shows that the elements of the neural ridge take the place, as we have seen, of specialized epithelia such as are found in the rain-worm's skin. These special sensory cells of the epidermis send a process into one of the ganglia of the ganglionic chain. (See Fig. 2.) In other worms the 'sensory' nerve-cell has its cell-body *beneath* the epidermis, one process terminating in the skin and the other in a ganglion of the ganglion-chain. This is on the whole the type of the greatest number of afferent nerve-elements of the vertebrates, the only exceptions being the olfactory and the optic apparatus, of which the former follows the type of the afferent elements in *Lumbricus*, the cell-body of the olfactory nerve fibre being among the epithelial cells of the Schneiderian membrane. Only few afferent elements seem to have their cell-body in the wall of the neural tube, as for instance the mid-brain root of the fifth nerve. The *Amphioxus* stands quite alone in having no neural ridges; all the afferent elements (spinal ganglion elements) have their cells in the wall of the neural tube.

The vertebrate body is to a certain degree segmented. This is clearly shown in the general aspect of the nervous system. We can divide the body by transverse sections into laminae which show a certain harmony of architecture within the region of the vertebrae, and, for our purposes, especially by the peripheral nerve-roots which come forth through the intervertebral foramina. The constant repetition of the type: vertebra-nerve-root-vertebra with the corresponding piece of the neural tube 'belonging to' the nerve-root constitutes the justifi-

cation for the term 'segment'. In the cranial region the principles for a plan of segmentation are more varied; the origin of the cranial nerves is more complex than that of the spinal ones; the segmentation of the skeleton is indistinct (we only remind of the controversy on the vertebral theory of the skull since Goethe's attempts of demonstrating a fusion of vertebræ in the skull), and the complication of the neural tube is greater than in the spinal segments owing to the complex sensory-motor mechanism of the head and owing to the centralization of certain general mechanisms which help to form the 'brain'. We should however deprive ourselves of many useful analogies if we should give up the segmental method in the cranial part of the neural tube on account of these difficulties. From an architectural point of view we do better to give up the term 'brain' which means the entire intracranial nerve-mass and to dissolve it into '*cranial segments*' and '*supersegmental parts*'. In this way we obtain for the entire nervous system the following plan of elements:

1. Segmental neurones—the sensory and the motor nerve-elements belonging to a segment (the 'peripheral nerve' neurones and their 'nuclei' in the neural stem).
2. The intersegmental neurones—nerve-elements which merely connect various segments among one another (forming largely the ground-bundles and the *formatio reticularis*).
3. The supersegmental neurones, constituting the cerebellar, midbrain and forebrain mechanism with their afferent and efferent connections with the segments.<sup>1</sup>

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<sup>1</sup>It is to be regretted that the term 'segment' has been used figuratively for parts which cannot thus be cut out. Gowers, for instance, speaks of a cerebro-spinal and a spino-muscular segment of the motor path. In order to avoid confusion, we shall, in the following, reserve the term 'segment' for the purpose of morphological divisions as described above. We do not, however, imply by this an accurate segmentation in the sense of the metamerism of embryology, but merely a functional topographical and 'practical' division. In principle the division is alike; but one of my segments may include several metameres. P. Argutinsky has shown (*Arch. f. mikr. Anat.*, Vol. 48, 1896) that a real ganglioform segmentation of the motor cells and of the cells of Clarke's column as claimed by certain writers does not exist, but that certain intermediate cells



A glance at the neural tube of the embryo, represented in plate II of His, zur Geschichte des Gehirns, and the figures 6-11 of the same work shows us that the cranial part is naturally divided into three enlargements, the hind brain (the part connected with the spinal cord, later called medulla and pons with the cerebellum covering the 'fourth ventricle'), the *mid-brain* (around the aqueduct of Sylvius) and the *forebrain* (around the third ventricle and its projections). Plate II of His gives a good idea of the distribution of the morphological segments of the entire *neural stem* (brain-stem and spinal cord).

For an easily comprehensible description of the details of internal structure of this 'neural tube' composed of spinal cord plus brain, we should give a more fully illustrated résumé of the contributions of His. For the present purpose I limit myself, however, to the following sketch of a plan of function and architecture of the nervous system which we shall use as a working basis for the study of the neurones. Moreover we refer to the summary from His on p. 121.

The figures 3, 4 and 5 of our plates form our starting point, the former from an early stage of human embryonic life (His), giving an idea of the evolution of the various cell-types, the latter from an embryo of *Pristiurus* (v. Lenhossék) illustrating the sensory-motor mechanism of one segment.

In the cross-section of the foetal oblongata (Fig. 4) the cells are found developing into various types; a certain number remain a simple endothelial lining of the neural canal—ependyma—other cells of a similar type are scattered throughout as cells of the frame-work or neuroglia; others become more and more highly developed, and form the various types of nerve cells proper.

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(Waldeyer's *Mittelzellen*) and, to a less extent, the lateral horn cells in the thoracic cord, are arranged in bead-like accumulations but without a relation to the root-segments. An explanation is not offered. *The readers of this essay will find that the terms 'segmental' as used here is usually synonymous with the term 'peripheral' as it is used generally; but it means spinal peripheral, including the whole of the peripheral neurones and their connections within the neural tube but with the exclusion of the cerebral and cerebellar mechanisms.*

The median line on the ventral side is usually called *raphe*; the portion next to it, the *ventral* or *basal lamina* of the tube, develops the *motor neurones*, the cells which send their fibers into the muscles, and *cells of an intersegmental character*, the processes of which do not leave the neural tube but grow in a longitudinal course into other segments (ground-bundle-cells). The *dorso-lateral part* of the tube-wall (also called wing-plate) receives the central termination of the afferent neurones, the cells of which are located in the ganglia outside. This dorso-lateral part, or posterior horn, contains cells which belong to the order of intermediate cells or shunt-cells. We shall see later on, how these intermediate cells become more specialized.

Looking at an entire row of segments of the neural tube, we find the following general arrangement: a small point of the skin is connected by an afferent nerve-element with the corresponding segment of the neural tube (spinal cord or brain-stem). One process of the cell reaches the skin; the other process grows as a fiber of the posterior root into the dorsal part of the neural tube. Directly after entering, it divides into a branch which runs towards the head and one which runs towards the caudal segments. Each branch gives off collaterals which terminate in various parts of each segment: some of them in the dorso-lateral plate, ending among shunt-cells, others in the ventral or motor plate, among the motor neurones. As in the worm, we see *one afferent neurone reaching many motor cells and many shunt-cells*. This is of great importance as is readily seen from this consideration: Each motor neurone is connected with certain definite muscle-fibrils on which it ends as end-plate. If these muscle-fibrils belong to a flexor muscle, the neurone might be called flexor-neurone, if the muscle is an extensor or rotator or abductor or adductor, the neurones belonging to each respectively are extensor, rotator, abductor, or adductor neurones. Now it is very probable that a sensory neurone supplying the volar side of a thumb gets into contact with sets of motor neurones connected with the *various* groups of muscles of the thumb. You might suppose that, if this were really the case, a stimulation of any part would call forth

a contraction of all of these muscles. This is indeed more or less true in abnormal conditions as I have seen in a patient, who went into a diffuse spasm of all the muscles as soon as he was startled by a touch. In the normal however we find that certain forms of stimuli call forth certain movements. You touch the thumb with a feather, the natural result will be that the thumb moves towards the index finger to press the object between the two fingers. This means that a certain quality of stimulation throws the sensory neurone into such a state of activity as will appeal to, and arouse, the motor neurones connected with the muscles which bring the thumb and index together. If however a needle or another cutting or pricking object is held against the thumb, the same sensory cells are put into a qualitatively different state of activity, to which the motor neurones of the above muscles have unlearned to react, but which arouses the antagonists, those which draw the finger from the object. The fact that so many motor cells are directly or indirectly connected with each sensory neurone, makes such a great variety of movements possible after different kinds of irritation of one and the same sensory neurone. In reality, far more complicated movements are possible. For the great variety of combinations of the muscles of even one segment, the help of the intermediate cells becomes essential; for a sufficient working together of all the segments in the body this is even more evident.

In order to give an idea of the complication of all the necessary mechanisms of the whole organism needed for a satisfactory cooperation of all the muscles we pass in a hasty review the principal segments of the vertebrate. They are not all of the same dignity and importance. The segments of the neural tube supplying the tail are necessarily built differently from those supplying the extremities or the trunk or the head. Morphologically there is a striking harmony among the segments behind the skull, as far as the vertebral column extends. The function of these segments is relatively uniform, representing the locomotion, the movements of the trunk, and the extremities. But in the head, greater diversity prevails. As

we have seen, there is a primary morphological division into three 'vesicles' (the division into five vesicles had better be abandoned, since it is partly artificial and because it cannot be carried out with advantage). We recognize the rhombencephalon or hind brain, the midbrain and the forebrain (thalamus and hemispheres). From a physiological and architectural point of view, we recognize in this 'brain' elements of segmental connections, and further the special supersegmental mechanisms, the cerebellar, midbrain, and forebrain apparatus.

In the human brain, we can conveniently outline the following *cranial segments*:

1. Those of the mechanisms of respiration, of articulation and of deglutition. The hypoglossal nerve supplies the muscles of the tongue; the pneumogastric, the viscera of the neck, thorax and abdomen, and the glossopharyngeal makes the connections for the reactions to stimulation of taste. These mechanisms are located in the body segments belonging to the lower part of the medulla oblongata or hind-brain.

2. The auditory-facial-abducens segment. Here we find on the 'sensory' side the auditory nerve in connection with the cochlea of the inner ear, and the equilibration (?) nerve, in connection with the semicircular canals, the sense organ for certain auditory qualities and 'appreciation of position in the space.' We know that destruction of the two produces deafness and dizziness and inability of equilibration. The motor side of this segment is represented by the facial nerve which moves the skin and muscles of the face, and, especially in animals, the external ear; and the abducens nerve, which moves the eyeball outward. It is easy to remember the function of this segment in this way; you hold a watch near the ear of a dog and he will prick up his ear and turn the eye to the side; the additional movement of the head depends on an association mechanism with other segments.

3. A little further forward we come to the segment of mastication. There we find the motor neurones for the muscles moving the jaw, and on the sensory side the large Gasserian ganglion which supplies most of the head with sensory fibers,



not only the mouth but also the other parts of the face and the mucous membranes of the head. Just this afferent nerve of the face teaches us a good lesson for the general arrangement of the sensory-motor mechanisms. We find that it spreads over the neurones for the movement of the jaws, the movement of the facial muscles, the tongue and even into the segments of the neck (by the 'ascending' root). Thus a prick of the cheek can be responded to directly by a movement of the jaw, of the muscles of the face, and of the entire head by the muscles of the neck.

These segments constitute the hind-brain, an important accessory organ of which we shall recognize presently in the cerebellum.

4. The mid-brain enlargement contains as a segmental mechanism the optic nerve and the nerves for the remaining muscles of the eyeball: the optic segment.

5. The forebrain contains only an afferent nerve-apparatus, the olfactory which is only in indirect communication with the various motor neurones.

This is a summary of the neuro-muscular segments which constitute the human body. How are they connected?

A study of the lowest vertebrate, the *Amphioxus*, may show how the various segments of the body can be very simply united for conjoint action. There are of course first the ground bundle-elements or intersegmental neurones. In the head end of the neural tube there are a few very large cells sending big fibers towards the caudal segments; and in the caudal end there are also a few large cells making connection with the segments of the head end. The cells are sufficient, together with the intermediate cells between the neighboring segments, to represent the coordination of movement of the *Amphioxus*. Such a simple mechanism would not suffice for the higher vertebrates. The number of such long connecting cells would be immense, considering the variety of complex movements of which we are capable. On the plan of the *Amphioxus* our nervous system would consist of the anterior horn cells and their fibers to the muscles, of the afferent ganglion cells and their fibers into the

skin and into the posterior horns. Each segment is connected with its neighbors by ground bundles. The immense multiplicity of sensory-motor combinations would require an immense number of long fibers running back and forth and the nervous system would have the form of a fairly uniform thick-walled tube. The function would be slow and complicated. In reality the results of coordination are obtained much more easily by centralization of the mechanisms which represent special functions.

We have seen that the auditory-facial-abducens segment contains an apparatus for equilibration. The sense-organ is formed by the semicircular canals of the internal ear, destruction of which leads to disorders of equilibration. Over this segment the mechanisms relating to the appreciation of coordination and equilibration of all the segments are united in a special structure, the *cerebellum*. It varies in size and complexity in the vertebrate series and is most developed in the fish, the birds and in man. Mechanisms which are scattered all over in the *Amphioxus* are thus centralized and can become more elaborate by short association elements within the special organ.

Further we find the optic segment (mid-brain) with a peculiar system of connections with the afferent elements of the rest of the body. In many animals which depend very largely on vision, as the trout, certain reptiles and especially birds, the mid-brain is very large and 'sensory' paths are connecting all the rest of the neural tube with it, so that all the afferent impulses can be elaborated into one harmonious entity.

Between the olfactory segment and the optic segment a further highly complicated mechanism develops, especially from the reptiles up, the thalamus and the fore-brain, most highly organized in man, and the organ of the highest reactions of which a living being is capable, among others the mental activity, thought, and reasoning.

Without entering on the detailed structure of the cerebellar, mid-brain and fore-brain mechanisms, I merely illustrate the principle of the cerebellum and the fore-brain.

Each *segment* of the neural tube has certain connections

with the cerebellum. Certain of its (intermediate) cells send their fibers into the cerebellum. These cells are most numerous where the nerve specially concerned in equilibration comes in; they are next in number in the segments of the lower part of the back (columns of Clarke) and in the external nucleus of Burdach. All the fibers end near the surface of the cerebellum, where the coordination elements of all the segments are brought near one another. The cerebellum then contains cells which influence directly or indirectly the motor elements of the various segments, and establish the necessary coordination. The neurones which have their cell-body in the segments and their fiber arborization in the cerebellum, are called *afferent cerebellar neurones*; the ones which have the cell-body in the cerebellum and the fiber arborization in the segments, *efferent cerebellar neurones*.

The supersegmental part of the mid-brain, on the main the corpora quadrigemina, has a great number of *afferent neurones*; in lower animals almost every segment sends fibers to meet the optic apparatus in the mid-brain; but in man the afferent mid-brain neurones are limited largely to the auditory segment (lateral fillet) and few fibers of Gowers' bundle (Mott). *Efferent neurones* of the mid-brain are not known with certainty (see however Bechterew<sup>1</sup>).

The most important extrasegmental mechanism is however that which grows up between the olfactory and the optic segments. We know it as *cerebral cortex and basal ganglia*, or cerebral mechanisms. Here too we find *afferent neurones* from each segment of the neural stem. These neurones are however already 'centralized.' It is commonly known that the afferent cerebral fibers for the spinal segments have their cells grouped together in the Nuclei of Goll and Burdach, at the point where the head segments go over into those of the neck. The peripheral sensory cells of the more caudal segments send their fibers all the way to meet them; they form the posterior

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<sup>1</sup> W. Bechterew, Ueber centrifugale aus der Seh- und Verhügelgegend ausgehenden Rückenmarksbahnen. Neur. Centralbl. No. 23, 1897.

columns of the spinal cord, the fibers from the segments of the lower extremity next to the median line, those from the brachial segment to their side, and finally those of the head yet further to the side as is seen from the drawings of the cord and medulla oblongata.

After an interruption and sifting in the optic thalamus, *secondary afferent elements* meet in the cortex the *cerebral efferent neurones* which form the pyramidal tract, the so called voluntary motor path, and their equivalents within the optic, auditory, etc., region. The forebrain is an exceedingly complicated mechanism; as one would expect from the tremendous complication of all the conscious activity of which we are capable, its differentiation apparatus is very elaborate.

There remains to be mentioned, that the higher mechanisms, cerebellum, midbrain and forebrain have connections among one another, not drawn in the chart (Fig. 6) in order not to complicate the drawing. Further we must say that this preliminary sketch of three supersegmental apparatus will require subdivisions and perhaps even additions in number. They are units only in the most general way, and given here as the types now most important.

This outline will, I hope, make clear the general point of view. It can perhaps be more forcibly illustrated in the following manner:

We saw that Forel formulates the laws of v. Gudden's degeneration experiments as follows: if a cell body is removed, the fiber belonging to it will degenerate, if a fiber termination in the central nervous system is cut, where regeneration is impossible the whole cell will atrophy slowly, and, in the case of the new-born at least, degenerate and disappear.

In accordance with the fundamental laws of the pathology of the central nervous system, we would therefore formulate our general point of view in this manner:

The phylogenetically oldest mechanisms are the sensory-motor apparatus constituting the purely segmental nervous system as defined above. Over them, lifted out from them for topographical centralization, there are specialized mechanisms,



the cerebellum, 'midbrain' and 'forebrain' supersegmental mechanisms. v. Monakow has been the first to speak of the forebrain and its *dependent elements* (*Grosshirnanteile*). When he cut a part of a forebrain, he killed not only the cells which he removed, and the fibers growing from them, but also cells located in other parts which send their fibers into the piece cut out. These latter elements he calls *Grosshirnanteile* with the same right as for instance the pyramidal tract; they are the afferent elements of the part, while the pyramidal tract is the efferent. I would generalize this principle and search for the 'Cerebellaranteile,' afferent and efferent elements of the cerebellum etc. For purely anatomical purposes it is indeed the most stimulating principle. We speak of the corpus albicans and its 'Anteile' etc.

(A thoughtful reader will see between the above lines a definite concept of the 'meaning' (i. e. interpretation) of the interrelation of cell-elements, the discussion of which does not properly belong here. In the neurological cant, we are accustomed to speak of connections of neurones for the purpose of association. According to the above, we rather think of interrelations of neurones for the purpose of *dissociation* and *readjustment*. A neurone reaches with its processes many individuals of many types of neurones and the interrelation with these takes place in order to make possible the reflection of different reactions in response to different states of excitation of the neurone.

This assumption becomes plain when we try to explain the 'interruption of the fiber-tracts by gray nuclei,' as when we speak of the 'interruption of the 'sensory' path by the nuclei of Goll and Burdach.' These 'nuclei' contain cerebral and cerebellar afferent neurones. The cerebellar neurones pick out special elements of excitation; the cerebral afferent neurones pick out other elements of excitation, as it were, selecting out those which belong together; otherwise, there would be no 'need' for an interruption. The same holds for the thalamic nuclei; in fact, for all accumulations of cells, after the paradigm given on page 141. From a physiological point of view,

the differentiation, or dissociation, becomes more prominent; the association is naturally also implied by the anatomical arrangement.)

The practical and didactic value of the above plan of the nervous system is quite evident when we take as an instance a section of the nervous system. The first question after a general orientation as to the presence of a central canal and the distribution of gray and white matter is this: Are there any segmental elements—motor neurones and afferent neurones? Which segment do they belong to? Cord, medulla, midbrain, or which part of the neural tube? Are there any cells and fibers of the ground bundle (intersegmental) formation? Cerebellar dependent parts? Midbrain dependent parts? Cerebral dependent parts? Any non-classified elements?

[To be Continued.]

#### DESCRIPTION OF FIGURES.

##### *Plate XV.*

*Fig. 1. A.* Interrelation of afferent and efferent cells, according to Nansen (and Golgi).

*B.* Interrelation of afferent and efferent neurones in the cortex, according to the idea of van Gehuchten and Cajal. From Ramón y Cajal, *Nuevo concepto*, etc., 1893.

##### *Plate XVI.*

*Fig. 2.* Diagram of the nervous system of *Lumbricus*. From Schaefer, *Brain*, XVI, p. 154.

##### *Plate XVII.*

*Fig. 3.* Human embryo of 10 mm. length (see the cross-section of rhombencephalon). Development of the "segmental nervous system" perfectly plain. Supra-segmental mechanisms barely indicated as Anlage of the cerebrum and cerebellum. Afferent neurones blue, efferent neurones red. His, *Geschichte des Gehirns*, Plate II.

##### *Plate XVIII.*

*Fig. 4.* Cross-section of the rhombencephalon of a human embryo 10 mm. long, x 40. Motor pneumogastric and hypoglossal nuclei with "ascending"

afferent pneumogastric root. To the left, isolated presentation of n. X and XII. Neither the olives and cerebellum nor the fillet and pyramids developed. Stage when only the segmental apparatus is plain. Roof of fourth ventricle (hind-brain cavity) membranous. Lateral lamina receiving the "sensory" (afferent) fibers of the nerve, and containing intermediate cells, cerebral afferent cells and especially the Anlage for the cerebellar apparatus (olives and cerebellum). Basal lamina with nucleus and nerve and numerous intermediate elements for the formation of the substanta reticularis. Adapted from W. His, *Zur Geschichte des Gehirns*, Fig. 21, p. 360.

*Fig. 5.* Central part of a spinal segment of *Pristiurus*. From Lenhossék. Afferent elements blue, efferent elements brick red. Intermediate elements omitted. Lateral lamina with the afferent terminations; basal lamina with the segmental motor neurones to the side of the raphe.

*Plate XIX.*

*Fig. 6.* General plan of the nervous system. Afferent segmental system blue, efferent (motor) segmental system brick red; cerebral mechanisms, afferent green, efferent carmine; cerebellar mechanisms, afferent yellow, efferent not shown.

A REPORT OF THE NEUROLOGICAL SEMINAR OF  
THE MARINE BIOLOGICAL LABORATORY,  
WOOD'S HOLL, MASS. SEASON OF 1898.

The Neurological Seminar was organized during the summer of 1896, with the object of bringing together in an informal manner those engaged in the investigation of the Morphology, Physiology or Pathology of the Nervous System. Meetings one hour in length, were held twice each week. Reports were presented embodying the results of personal research or the critical review of the literature of the subject under investigation. Demonstrations and drawings were used to illustrate the points presented and prepare the way for discussion.

During the first season the attendance was restricted to the active members, of whom there were twenty. The second season, 1897, there was no increase in the number of members; about half the entire number had participated in the meetings of the previous season. The subjects discussed can be grouped under a few main heads. The investigation of the lateral line of vertebrates, its innervation and the relation of its sense organs to the organs of special sense has held the first place. Only second to it was the question of metamerism in the vertebrate head and in the nervous system of annelids. The subject of equilibration has received much attention from the physiologists.

The present season the meetings have been made public and the neurologists at the Biological Laboratory of the United States Fish Commission were invited to take active part. The membership has advanced to thirty six, although only twenty nine presented reports, the others being prevented from doing so by various causes.



Through the kindness of Dr's. Parker and Montgomery the Seminar enjoyed the privilege of studying Professor Apáthy's slides, illustrating his paper on the finer structure of the nervous elements. (Mitt. Zool. Sta. Neapel, Bd. 12, Heft 4.) The great scientific value of the slides and importance of the facts demonstrated were fully appreciated by both the neurologists and investigators in other departments. An entire afternoon was given to the study and comparison of the slides and a hearty vote of thanks was tendered to Professor Apáthy by the Seminar. This action was cordially endorsed by all who examined the slides.

A demonstration was also given by Dr. C. F. Hodge of the structural differences between the pyramid cells from the brain of a sleeping puppy and the corresponding cells from the cerebral cortex of a puppy of the same litter which had been fatigued before killing.

#### PROGRAM.

July 14.

C. JUDSON HERRICK, *Denison University and Pathological Institute of the New York State Hospitals.*

The Cranial Nerves of the Bony Fishes.

T. W. GALLOWAY, *Brownsville, Penna.*

Some Nervous Changes Accompanying Budding in *Dero vaga*.

July 19.

MISS C. M. CLAPP, *South Hadley, Mass.*

Review of Allis' Paper on the Cranial Nerves of *Amia*.

H. V. NEAL, *Knox College, Galesburg, Ill.*

The Problem of the Vertebrate Head.

July 21.

T. H. MONTGOMERY, JR., *Philadelphia, Pa.*

The Elements of the Central Nervous System of the Nemertians.

U. DAHLGREN, *Princeton, N. J.*

The Giant Ganglion Cell Apparatus.

A. D. MORRILL, *Clinton, N. Y.*

Innervation of the Olfactory Epithelium.

July 26.

MRS. M. L. NICKERSON, *University of Minnesota.*

Epidermal Organs of *Phascolosoma gouldii*.

MISS ANNA MOORE, *Poughkeepsie, N. Y.*

Review of Papers on the Nervous System of Dinophilus.

W. W. NORMAN, *Austin, Texas.*

Bethe on Forced Movements in Arthropods.

August 2.

Demonstration of Apáthy's Slides.

T. H. MONTGOMERY, JR., *Philadelphia, Pa.*

Review of Apáthy's Paper on Primitive Fibrils.

G. H. PARKER, *Cambridge, Mass.*

Influence of Apáthy's Conclusions on the Neuron Theory.

August 4.

MISS J. A. HAYNES, *Troy, N. Y.*

Review of Literature on Sympathetic Nervous System of Annelids.

PORTER E. SARGENT, *Cambridge, Mass.*

The Giant Ganglion Cells in the Spinal Cord of *Ctenolabrus coeruleus* (Storer).

W. C. JONES, *Evanston, Ill.*

Report, Huber's Paper on the Sympathetic Nervous System of Vertebrates.

CRESSWELL SHEARER, *Westmount, Montreal, Canada.*

On the Nerve Terminations in the Selachian Cornea.

August 5.

F. C. WAIT, *Cambridge, Mass.*

Variations in Lumbo-sacral Plexus of *Necturus maculosus*.

G. W. HUNTER, JR., *Hyde Park High-school, Chicago, Ill.*

Notes on The Peripheral Nervous System of *Molgula manhattensis*.

L. E. GRIFFIN, *Baltimore, Md.*

Tentacular Nervous System of *Nautilus*.

S. R. WILLIAMS, *Cambridge, Mass.*

Review of Hamaker's Paper on the Central Nervous System of *Nereis*.

August 6.

C. F. HODGE, *Worcester, Mass.*

Demonstration showing Differences between resting and fatigued pyramidal Cells in the Puppy.

August 9.

O. S. STRONG, *Columbia University, New York.*

Review of Johnston's Paper on the Cranial Nerves of the Sturgeon.

C. R. BARDEEN, *Johns Hopkins Hospital, Baltimore, Md.*

On Variations in the Distribution of the Spinal Nerves Entering the Lumbar Plexus.

C. W. HARGITT, *Syracuse, N. Y.*

Review of Conant's Paper on Cubomedusæ.

E. W. BERGER, *Johns Hopkins University, Baltimore, Md.*

The Histological Structure of the Eyes of Cubomedusæ.

August 11.

E. P. LYON, *Peoria, Ill.*

Functions of the Otolith.

IRA VAN GIESON, *Pathological Institute of the New York State Hospitals.*

Effects of Starvation on the Nucleus of Ganglion Cells.

H. R. FLING, *State Normal School, Oshkosh, Wis.*

A Contribution to the Nervous System of the Earthworm.

F. L. LANDACRE, *Ohio State University, Columbus, O.*

Demonstration of Preparations of Teleost Brain.

E. RYNEARSON, *Central High-school, Pittsburgh, Pa.*Review of Paper on the Nervous System of *Arenicola marina*.

Among the members of previous seasons are Miss Fanny E. Langdon, Miss M. L. Nichols, Miss M. M. Sturgess, Drs. H. Ayers, C. L. Bristol, G. P. Clark, C. W. Green, J. H. Gerould, A. Graf, B. F. Kingsbury, W. A. Locy, P. C. Mensch, W. A. Patten, S. Paton, and A. Schaper, Messrs. G. L. Houser, J. B. Johnston, V. E. McCaskill, J. E. Peabody and O. H. Swezey.

A. D. MORRILL,  
*Chairman.*

## THE PROBLEM OF THE VERTEBRATE HEAD.

By H. V. NEAL.

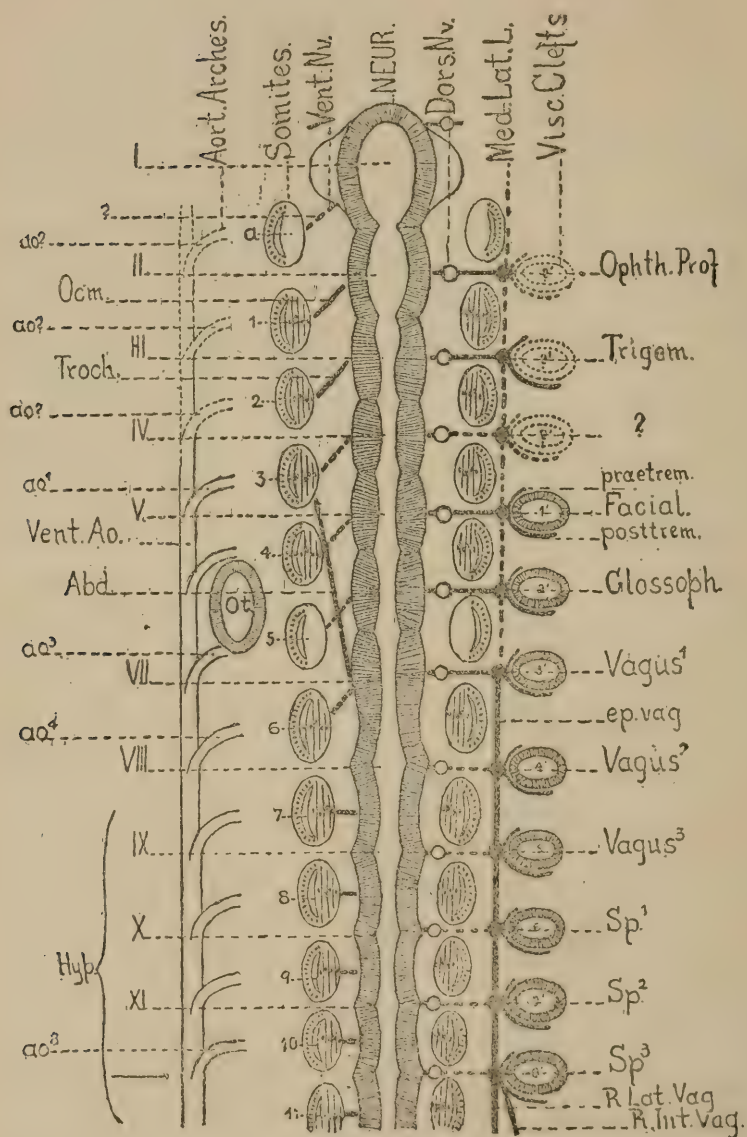
Knox College.

Two of the most important morphological conceptions of the nineteenth century are attributed to the poet Goethe—one, that a flower is a modified branch and its organs metamorphosed leaves—the other, that the head and trunk of vertebrated animals were once composed of like segments which by slow adaptive change have become to a considerable degree unlike. After a century of probation no morphologist of today questions the truth of the former conception. The truth of the latter, however, is still debated and the attempt to compare a head segment with a trunk segment in vertebrates constitutes what is now known as the “head problem.”

Since neither head nor trunk can be regarded as *primitive* in their present condition, probably a more correct statement of the problem would be as follows; Was the vertebrate head like the trunk, primitively segmented; if so, were these segments serially homologous with those of the trunk; and how many have entered into the composition of the head? So far as I am aware, no one doubts that the vertebrate head is segmented. That it is so, is indeed clearly evinced by such serially repeated organs as neuromeres or segments of the central nervous system, nerves both dorsal and ventral, somites, visceral clefts, visceral arches and aortic arches.

But while the great majority of the morphologists who have expressed an opinion on the question have concluded that Goethe's conception is true and that head segments are serially homologous with trunk segments, a few have been led during recent years to regard the head, or at least its anterior or pre-otic part, as one *sui generis*. This conclusion has been reached partly by the recognition of the considerable differences between head and trunk metameres and the organs of which they are composed—differences which seem too great to be merely differences in the degree of specialization and partly also by the





conflicting evidence and conclusions, both as to composition and number of cephalic segments, of those who have advocated the prevalent morphological opinion. Of the differences stated by them I shall speak later. The confusion in, and, as must be admitted, generally unsatisfactory condition of the literature bearing on the head problem, is in my judgment attributable in great part to the fact that the observations of investigators have been confined often to a single species, often to a single organ system, while their conclusions deduced from such limited observations have applied to the *phylogenesis of the entire vertebrate head*! That such methods are inadequate for the solution of such a difficult problem seems in view of the many divergent opinions too obvious to need insistence here, and I venture to predict that some time, if not now, it will seem strange that a morphologist should assume, or seek to demonstrate that the serial parts of any single organ system, whether neuromeres, or nerves, or somites or visceral arches, or epibranchial "sense organs," or what not, are the *essential* criteria of head segments. In my opinion, *phylogenetic conclusions concerning the metamerism of the head based upon the study of a single animal or a single organ system need to be "controlled" and confirmed by the study of other organ systems in the same animal.* The solution of no problem requires a broader knowledge of comparative embryological and anatomical facts.

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*Fig. 1.* Diagrammatic representation of the cephalic metameres in Selachii, showing the component organ systems and their relations to one another.

*I-XI*, cephalic neuromeres (segments of the central nervous system); *a*, Miss Platt's "anterior" somite; *1-12*, van Wijhe's first to twelfth somites; *1<sup>1</sup>-8<sup>1</sup>*, first to eighth visceral clefts; *abd.*, abducens; *ao<sup>1-8</sup>*, aortic arches, first to eighth; *ch.*, chorda; *dors. nv.*, dorsal nerve; *ep. vag.*, epibranchial portion of vagus nerve; *fac.*, facialis nerve; *glossoph. (gls.)*, glossopharyngeus nerve; *hyp.*, hypophysis; *m.*, mouth; *med. lat. l.*, mediolateral line; *neur. (n.)*, neuromere; *oem.*, oculomotorius; *olf.*, olfactorius; *ophth. prof. (pf.)*, ophthalmicus profundus nerve; *ot.*, otic capsule (ear); *posttrem.*, posttrematic branch; *praetrem.*, praetrematic branch; *r. lat. vag.*, ramus lateralis vagi; *r. int. vag.*, ramus intestinalis vagi; *som.*, somites (van Wijhe's): *sp.<sup>1-3</sup>*, spinal ganglia first to third; *troch.*, trochlearis; *vent. ao.*, ventral aorta; *vent. nv.*, ventral nerve; *visc. clefts*, visceral clefts; *vag.<sup>1-3</sup>*, vagus ganglia first to third (dorso-lateral series); *visc.<sup>3</sup>* third visceral arch. The arrow marks the posterior termination of the cranium in *Squalus*. All neuromeres anterior to this point are included in the cranium.

Holding this view, I have recently<sup>1</sup> made an attempt to solve the head problem, and while my observations were made primarily upon the nervous system in Selachian embryos, my theoretical conclusions have been controlled by the study of the actual relations of other organ systems and also by the study of embryos of all other classes of vertebrates except Reptiles. Whether or not I have come nearer a solution of the head problem than have many of my predecessors, depends, I am convinced, on whether or not I have adhered with greater fidelity than they to the principle above enunciated. I regard my results as in great part a confirmation of those of van Wijhe ('82) and valuable as such.

First, as regards the *nature* of cephalic metameres, I conclude with the majority of investigators that they are serially homologous with trunk metameres, although the homology is today but partial. To my mind, the differences which have been considered as objections to this view by certain morphologists, such for example as the fact that (*a*) visceral clefts and arches are confined to the head region (Gegenbaur); that (*b*) excretory organs are confined to the trunk region; that (*c*) there are no somites in the head, at least in its pre-otic portion, (Kastschenko, Rabl, Froriep); that cephalic nerves and spinal nerves cannot be compared by reason of the fact that (*d*) cephalic dorsal nerves receive cellular material from the skin, while spinal dorsal nerves do not; that (*e*) cephalic dorsal nerves are mixed, while spinal dorsal nerves are sensor in function; that (*f*) cephalic dorsal nerves extend lateral, and spinal dorsal nerves median, to the somites; that (*g*)—at least some—cephalic dorsal nerves have component sensor fibers which innervate lateral line organs, while in spinal nerves these are wanting; that (*h*) in one and the same occipital metamere there can be found (1) a cephalic dorsal nerve, (2) a spinal dorsal nerve, and (3) a spinal ventral nerve and that therefore spinal and cephalic

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<sup>1</sup> NEAL, H. V., '98. The Segmentation of the Nervous System in *Squalus acanthias*—A contribution to the Morphology of the Vertebrate Head. Bull. Mus. Comp. Zool. Harvard Univ., Vol. 31, No. 7, pp. 145-294, with nine plates.

dorsal nerves cannot be of the same kind; and other less important differences by no means outweigh the evidence of similarity of head and trunk segments.

As a <sup>↑</sup>matter of fact some of the differences alleged above do not actually exist. Many, it is noted, apply to the nerves, and these have seemed so great that even Gegenbaur, the early champion of the present morphological conception of the vertebrate head states ('87) that he is no longer able to consider cephalic and spinal nerves as homodynamous. With our present knowledge, however, that in *Amphioxus* two kinds of nerves, viz. dorsal mixed nerves whose motor fibers innervate splanchnic musculature, and ventral motor nerves which innervate somatic musculature, are found in each segment of the body except the first; that in *Craniota* both of these kinds of nerves appear in the head as well as in the trunk; that a pair is to be found in each trunk metamere (in *Petromyzon* unconnected as in *Amphioxus*), and in some head metameres, I am unable to regard the actual differences between cephalic and spinal nerves as fundamental in character.<sup>1</sup>

The differences which appear are, in my judgment, to be expected in the case of the nervous organs in such highly differentiated structures as head and trunk. Furthermore, the fact that the bounds of head and trunk in the vertebrate series are not definitely fixed; that they are variable; that there is an unbroken continuity throughout head and trunk of such essential components of metameres as neuromeres, nerves, somites, visceral arches, visceral clefts, and aortic arches, is evidence sufficient to warrant the general belief in the serial homology of the segments in these two regions. So far as I can see, no objections to this view apply to the pre-otic region which are not equally applicable to the post-otic region. If the segments in the one region are serially homologous with trunk metameres, those in the other region are also. I shall be obliged to refer the

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<sup>1</sup> The evidence both histological (Lenhossék, Kölliker, Ramón y Cajal) and physiological (Steinach and Wisner) given in the last decade, seems to establish conclusively the fact (rendered *a priori* probable by the evidence from *Amphioxus*) that spinal dorsal nerves are like cephalic dorsal nerves mixed in function.



reader for further grounds for my conclusions concerning the nature of head segments to the more extended paper referred to above.

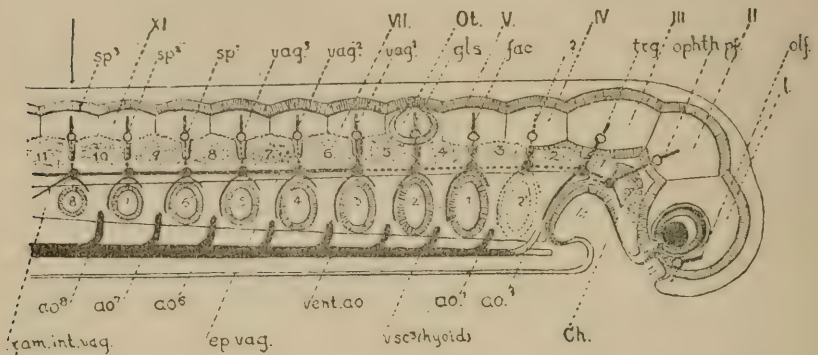


Fig. 2. Diagram of Selachian head, showing the cephalic metamereres and their components, lateral aspect, based upon the study of *Squalus acanthias*. Upon the basis of the results of Kupffer, Miss Platt and others a distinction is made in the representation of dorsal nerves between dorso-lateral and medio-lateral (epibranchial) ganglia.

Secondly, as regards *number* and *composition* of cephalic metamereres my conclusions have been summarized in Figs. 1 and 2. There are in vertebrates five pre-otic, one otic and (in *Squalus*) five post-otic cephalic metamereres. The number of post-otic segments whose vertebral components fuse into the occipital region of the cranium of vertebrates is variable. The estimate of the number of pre-otic segments is based chiefly upon the evidences that in this region of *Squalus* embryos neuromeres and somites *numerically correspond*, and are in some cases connected by motor nerves. For a more extended presentation of this evidence I again refer to the longer paper ('98). Briefly summarized, the composition of cephalic metamereres from the first to the last is as follows:

**METAMERE I.** *Neuromere*, neuromere I (primary forebrain vesicle); *dorsal nerve*, olfactory (motor component lacking—in correlation with the want of splanchnic musculature); *ventral nerve*, absent in correlation with the absence of somatic muscu-

lature; somite, "anterior" (Miss Platt's); *visceral cleft* and *arch*, hypothetical; *aortic arch*, hypothetical.

METAMERE II. *Neuromere*, neuromere II (primary mid-brain vesicle); *dorsal nerve*, ophthalmicus profundus (motor fibers absent in *Squalus*, but present in some vertebrates); *ventral nerve*, oculomotorius; *somite* van Wijhe's 1st; *visceral arch* and *cleft*, hypothetical; *aortic arch*, hypothetical.

METAMERE III. *Neuromere*, neuromere III (Hinterhirn); *dorsal nerve*, trigeminus; *ventral nerve*, trochlearis; *somite*, van Wijhe's 2nd; *visceral arch*, first (mandibular); *visceral cleft*, (bounding anteriorly the ventral portion of the segment) usurped by mouth; *aortic arch*, first (mandibular).

METAMERE IV. *Neuromere*, neuromere IV; *dorsal nerve*, hypothetical (absence correlated with the absence of a visceral arch); *somite*, van Wijhe's 3rd; *ventral nerve*, abducens; *visceral cleft* and *arch*, hypothetical; *aortic arch*, hypothetical.

METAMERE V. *Neuromere*, neuromere V; *dorsal nerve*, facialis (the acusticus a specialized sensor branch); *ventral nerve*, abducens; *somite*, van Wijhe's 4th (which together with the 3rd forms in *Torpedo* the m. rectus posterior, Sewertzoff—rudimentary in *Squalus*); *visceral cleft*, first (hypobranchial, spiraculum); *visceral arch*, second (hyoid); *aortic arch*, second (hyoid).

METAMERE VI. *Neuromere*, neuromere VI; *dorsal nerve*, glossopharyngeus; *ventral nerve*, abducens; *somite*, van Wijhe's 5th (myotome absent in *Squalus*; forms first myotome of the lateral trunk musculature in *Petromyzon*); *visceral cleft*, 2nd visceral (1st branchial); *visceral arch*, third (1st branchial); *aortic arch*, third.

METAMERE VII. *Neuromere*, neuromere VII (the last of the neuromeres having a lateral thickening. See Fig. 1); *dorsal nerve*, vagus<sup>1</sup>; *ventral nerve*, abducens; *somite*, van Wijhe's 6th (myotome rudimentary in *Squalus*); *visceral cleft*, third (second branchial); *visceral arch*, fourth; *aortic arch*, fourth.

METAMERE VIII. *Neuromere*, neuromere VIII; *dorsal nerve*, vagus<sup>2</sup>; *ventral nerve*, hypoglossus (anterior root, rudi-

mentary); *somite*, van Wijhe's 7th (myotome, first myotome of lateral trunk musculature in *Squalus*); *visceral cleft*, fourth; *visceral arch*, fifth; *aortic arch*, fifth.

METAMERE IX. *Neuromere*, neuromere IX; *dorsal nerve*, rudimentary (unites with vagus in *Squalus*); *ventral nerve*, hypoglossus, second root; *somite*, van Wijhe's 8th (forms first segment of hypoglossus musculature); *visceral cleft*, fifth; *visceral arch*, sixth; *aortic arch*, sixth.

METAMERE X. *Neuromere*, neuromere X; *dorsal nerve*, first spinal (represented by a rudimentary ganglion in *Squalus* embryos); *ventral nerve*, hypoglossus; *visceral cleft*, sixth; *visceral arch*, seventh; *aortic arch*, seventh.

METAMERE XI. *Neuromere*, neuromere XI; *dorsal nerve*, second spinal (rudimentary ganglion in *Squalus* embryos); *ventral nerve*, hypoglossus; *somite*, van Wijhe's 9th; *visceral cleft*, seventh; *visceral arch*, eighth; *aortic arch*, eighth.

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## THE CRANIAL NERVES OF THE BONY FISHES.

By C. JUDSON HERRICK.

The cranial and first spinal nerves of *Menidia* have been plotted by reconstruction from serial sections in order to exhibit the relations of the nerve components both proximally and distally. In most cases the several components have been traced from their nuclei of origin or termination in the brain through the ganglia to their peripheral termination.

Throughout the gnathostome vertebrates we now commonly recognize four components in the typical spinal nerve—(1) somatic motor, from the ventral horn cells; (2) somatic sensory (general cutaneous), terminating in the dorsal horn; (3) visceral motor; and visceral sensory. The central relations of the last two components are still obscure. They are probably both related to the "intermediate" or lateral horn zone, the sensory fibers coming in by the dorsal root and the motor fibers (in infra-mammalian groups, at least) going out by both dorsal and ventral roots.

Now in the bony fish the cranial nerves exhibit these four components and in addition a fifth, the acustico-lateral. The somatic motor is represented by the eye-muscle nerves; the somatic sensory by the general cutaneous component of the V and X nerves, terminating in the spinal V tract, which is the continuation of the dorsal horn of the spinal cord; the visceromotor by the motor fibers of the other cranial nerves, going out near the sensory fibers by dorsal roots to the branchial musculature. The viscerosensory system, like the visceromotor, has been hypertrophied and is represented by the communis system of the X, IX and VII nerves, terminating, either directly or through the mediation of the fasciculus communis in the vagal lobe (chief sensory vagus nucleus of higher forms). The communis system of the head, unlike the corresponding visceral sensory system of the trunk, receives fibers from taste buds and other sense-organs not belonging to the lateral line

system. The acustico-lateral system receives fibers from the ear and lateral line organs and no others. These fibers all terminate together in the tuberculum acusticum.

In the cranial nerves the motor fibers for the unstriated visceral musculature (with sympathetic connections?) are, as in the trunk, very small, while those for the striated visceral musculature of the branchial arches and for the somatic eye-muscles are large. The general cutaneous fibers are small or medium, the *communis* fibers are all very small, and of the acustico-lateral fibers those from the lateral line organs are for the most part very large, while the auditory fibers are of medium size.

The accompanying diagram exhibits the relations of the sensory components in the cranial nerves of *Menidia* and some of the more important points are reviewed in the following summary.

1. The *ramus medius* (r. *lateralis* of authors) of the spinal nerves usually anastomoses with a twig of the n. *lateralis vagi*; but in all cases the spinal fibers go to the skin around the lateral line, and never to a lateral line organ.

2. The *first spinal* is obviously a fusion of two segmental nerves, possibly of more than two.

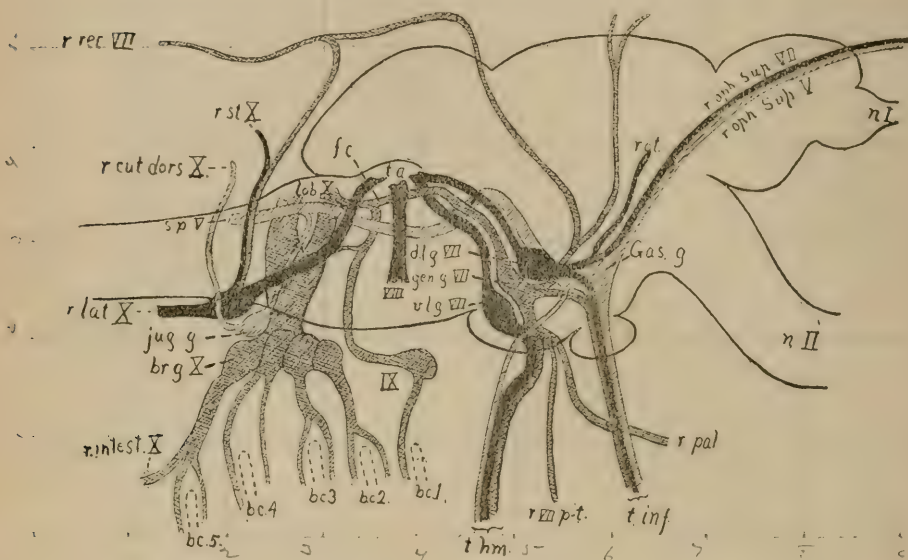
3. The *vagus nerve* contains *general cutaneous* fibers (*rami cutanei dorsales*), which have a special ganglion (jugular g. of Shore and Strong) and which terminate in the spinal V tract.

4. The *vagal lobe* is mainly, at least, the terminal nucleus for visceral sensory fibers and hence is to be regarded as the continuation into the head of the "intermediate zone" of the spinal cord, rather than of the dorsal horn, as some have maintained. These fibers, which will be termed *communis* fibers, are in part general visceral sensory fibers from mucous surfaces and in part fibers from more highly specialized organs—taste buds etc.

5. The nucleus ambiguus, giving rise to the *motor root of the vagus*, has been specialized away from the general visceromotor center in correlation with the development of the striated visceral musculature of the branchial arches. The central ner-

vous connections of fibers for the unstriated visceral musculature of the vagus region are obscure.

6. The *XI* nerve may be identified in teleosts. It arises probably from the caudal part of the nucleus ambiguus and



#### DESCRIPTION OF THE FIGURE.

A diagrammatic view of the sensory components of the cranial nerves of *Menidia*, as seen from the right side. The diagram is based upon a projection of the cranial nerves upon the sagittal plane made by reconstruction from serial sections. The general cutaneous component is indicated by the single cross-hatching, the communis component by double cross-hatching and the acustico-lateral is drawn in black.

#### REFERENCE LETTERS.

- b. c. 1* to *b. c. 5*.—The five branchial clefts.  
*br. g. X*.—The ganglia of the four branchial rami of the vagus, the last one containing also the ganglion of the *r. intestinalis*.  
*d. l. g. VII*.—The dorsal lateral line ganglion of the VII nerve.  
*f. c.*—Fasciculus communis.  
*Gas. g.*—Gasserian ganglion.  
*gen. g. VII*.—Geniculate ganglion of the VII nerve.  
*IX*.—The glossopharyngeal nerve and its ganglion.  
*jug. g.*—The general cutaneous ganglion of the vagus nerve—jugular g. of Shore and Strong.

supplies the trapezius muscle. It is apparently a visceromotor nerve.

7. The *n. lateralis vagi* terminates in the tuberculum acusticum, crossing all of the other vagus roots without, however, being connected with them in any way. It, however, receives a small bundle of communis fibers from the IX root. The latter, apparently go out with the first three or four branches of the *n. lateralis* (the first of these being the *r. supra-temporalis vagi*), accompanying the proper *lateralis* fibers, and ultimately anastomose with the *r. recurrens VII*.

8. The *sensory IX* is composed exclusively of communis fibers. They enter the lobus vagi by way of the fasciculus communis. Neither *lateralis* nor general cutaneous fibers are received during any part of its course, nor is there any connection with any other nerve save the sympathetic chain and the intra-cranial anastomosis with the root of the *n. lateralis vagi* already mentioned. The IX nerve lacks the *r. pre-trematicus* and the *r. supra-temporalis*.

9. The *motor IX* arises from the cephalic part of the nucleus ambiguus, runs for a considerable distance along the lateral

*lob. X.*—The lobus vagi.

*n. I.*—The olfactory nerve.

*n. II.*—The optic nerve.

*r. cut. dors. X.*—Ramus cutaneus dorsalis of the vagus.

*r. intest. X.*—Ramus intestinalis of the vagus.

*r. lat. X.*—Ramus lateralis of the vagus.

*r. oph. sup. V.*—Ramus ophthalmicus superficialis trigemini.

*r. oph. sup. VII.*—Ramus ophthalmicus superficialis facialis.

*r. ot.*—Ramus oticus.

*r. pal.*—Ramus palatinus facialis.

*r. rec. VII.*—Ramus recurrens facialis.

*r. st. X.*—Ramus supratemporalis vagi.

*r. VII p-t*—Ramus pre-trematicus facialis.

*sp. V. t.*—Spinal V tract ("ascending root of the trigeminus").

*t. a.*—The tuberculum acusticum.

*t. hm.*—Truncus hyomandibularis of the facial nerve.

*t. inf.*—Infra-orbital trunk, containing the *r. mandibularis V*, the *r. maxillaris V*, and the *r. buccalis VII*, together with communis fibers.

*VIII.*—The eighth nerve.

*v. l. g. VII.*—The ventral lateral line ganglion of the VII nerve.



surface of the fasciculus longitudinalis dorsalis and before leaving the latter contributes a considerable bundle of fibers to it.

10. The *auditory nerve* terminates in the tuberculum acusticum, and its fibers are internally so mingled with the lateralis fibers from the X and VII nerves that analysis is impossible in Weigert preparations.

11. The sensory VII roots contain two components. The *communis portion*, enters the fasciculus communis, comprising the whole of that tract except the fibers received from IX. It terminates in the lobus vagi, a lobus trigemini not being developed. This communis root enters the geniculate ganglion and distributes to (1) the r. palatinus (comprising the whole of that nerve) for the mucosa and taste buds of the roof of the mouth; (2) the truncus hyo-mandibularis VII for the mucosa and taste buds of the inside of the lower jaw and lip; (3) the r. maxillaris V to taste buds within the upper lip; (4) the r. recurrens VII. The latter fibers pass dorsally into the cranial cavity, forming in the meninges an elaborate plexus, finally to combine into the r. recurrens which runs the length of the body superficially near the dorso-median line. These communis fibers supply some terminal buds on the top of the head and some others probably run forward with the ophthalmicus superficialis. In addition to the above there is (5) a small twig which leaves the geniculate ganglion between the truncus hyo-mandibularis and the r. palatinus running directly ventrally to the roof of the mouth, supplying its mucosa in the region between the areas supplied by the IX and palatine nerves. In its course it passes along the cephalic face of and innervates the very large pseudobranch. This is the only nerve supply which that organ possesses, and this nerve is accordingly, I think, to be regarded as the pre-trematic VII nerve, the pseudobranch representing a spiracular gill and the truncus hyo-mandibularis the post-trematic VII.

12. The second sensory component of the VII nerve is represented by two *lateral line roots*. (a) The ventral lateralis root has a separate ganglion and supplies organs of the opercular and mandibular canals, via the truncus hyo-mandibularis. (b)

The dorsal lateralis root also has a separate ganglion and supplies organs of the infra-orbital and supra-orbital lines, via the r. buccalis and r. ophthalmicus superficialis VII respectively.

13. The nucleus of the *motor VII* corresponds in position and structure to the n. ambiguus and the root is related to the dorso-median fasciculus exactly like the motor IX root. It is, at its origin, distinct from the sensory roots of VII and supplies the mm. levator operculi, adductor operculi, adductor hyo-mandibularis, adductor arcus palatini and the branchio-stegal muscles, as usual among the teleosts. It does not, however, supply the m. genio-hyoideus, as usually stated.

14. The *sensory V* is composed exclusively of general cutaneous fibers. It receives the whole of the pre-vagal spinal V tract. The Gasserian is its proper ganglion and this term should not be applied to any other cells of the V + VII ganglionic complex. From the Gasserian g. are given off general cutaneous fibers into (a) r. maxillaris V, (b) r. mandibularis V, (c) r. ophthalmicus superficialis V, (d) fibers running back into the truncus hyo-mandibularis VII for the operculum, also (e) a very small r. profundus V. The latter accompanies the sympathetic fibers of the radix ciliaris longa of the ciliary ganglion to that ganglion after which they can no longer be separately followed. The relations of this nerve, which has not before been described for teleosts, indicate that the embryonic profundus ganglion has fused with the Gasserian.

15. The *motor V* nucleus resembles that of the motor VII, but lies farther laterad and dorsad. The fibers enter the r. mandibularis V and supply the mm. dilator operculi, levator arcus palatini, adductor mandibularis, inter-mandibularis and genio-hyoideus. The innervation of the latter muscle has hitherto been usually assumed to come in teleosts from the VII. This muscle is almost certainly not homologous with the muscle in the corresponding position of other vertebrates which is supplied by the 1 spinal or XII nerve.

16. The sympathetic chain has ganglia on nearly all of the cranial ganglia and probably sends fibers into all of the rami from

the latter. In passing from IX to VII ganglia the sympathetic runs external to the ear capsule.

The various components can be followed with great precision proximally in the root portions and through the ganglia of the cranial nerves. Throughout the peripheral courses of the nerves the analysis is somewhat more difficult, but has been satisfactorily accomplished in all but a very few cases. The naked organs of the lateral line series (pit lines) and the terminal buds of the skin (communis system) are sometimes hard to differentiate because their nerve fibers are intermediate in size between the exceedingly large fibers typical for the lateralis system and the very small communis fibers. The general cutaneous system of nerves is, however, as clearly separable from the others peripherally as it is centrally. And this is important in many ways. For example, it will materially assist in the attempt to homologize cranial and spinal nerves to know that not all sensory cranial roots are comparable with spinal dorsal roots. It is, e. g., no longer legitimate to homologize lateral line roots with dorsal spinal roots. The latter are represented in the brain mainly by the spinal V or general cutaneous system, and the special cutaneous systems (terminal bud and lateralis) are probably neomorphs in the head, as Strong has maintained.

If cranial and spinal nerves were derived from a common type, the common ancestral nerve probably contained two kinds of sensory fibers, viz. general cutaneous and general visceral. Both of these kinds of fibers appear to be present in the dorsal roots of *Amphioxus* and of the spinal nerves of *Craniota*. Two of the cranial nerves retain the general cutaneous fibers (viz. X and V); the others seem to have lost them. The viscerosensory fibers have either been lost or rendered unrecognizable on account of their extreme specialization in all but the X, IX and VII nerves. In these nerves they have been centralized to form the communis system and hypertrophied to serve a double purpose: (1) The viscerosensory nerves of the trunk seem to have been in large measure supplanted by the *r. intestinalis vagi*. (2) In the cephalic end of the digestive tract more highly specialized sense-organs (taste buds) have been de-

veloped in response to an obvious functional need. The advantage to be derived from such a centralization of the sensory apparatus of the entire digestive tract is obvious.

The acustico-lateral system is apparently phylogenetically the youngest of the cranial systems. Its relations to the other sensory systems are still problematical.

ADDENDUM. Since this paper was read there has appeared the very suggestive paper on the cranial nerves of the sturgeon (*Anat. Anzeiger*, XIV, 22-23) by J. B. Johnston. His conclusions, which differ somewhat from my own, I shall examine critically at another time, merely mentioning a few of the salient points here. Johnston identifies the general cutaneous and acustico-lateral systems, regarding them both as representing the dorsal horns of the spinal cord. The acustico-lateral is the more highly specialized part and it possesses a spinal portion running parallel with the spinal V, which he calls the spinal VIII. The close internal connections between these two systems and their close parallelism in many other respects certainly favor the belief that the acustico-lateral has been differentiated from the general cutaneous, in spite of the complete discreteness of the two systems peripherally. And it should be noted that this does not imply that the lateralis rami from the head can ever be directly homologized with any rami of spinal nerves; for the former are none the less neomorphs in the head, even though their precursors were in the spinal nerves, as Cole has so ably argued. It is interesting to note that the latter author also regards the acustico-lateralis system as the derivative of the general cutaneous, the evidence in this case being embryological.

Now, Johnston regards the communis system as peculiar to the head, having no spinal representatives. He even goes so far as to state that "no sensory fibers of the spinal nerves supply visceral structures." This, I think, is erroneous, even in the higher forms, though the great reduction and profound modification of the viscero-sensory system of the trunk under the influence of the r. visceralis vagi are freely granted. Further-



more, Johnson regards this communis system as exclusively visceral, i. e. entodermal, and opposes to it the other sensory system, viz. the general cutaneous and acustico-lateral, as related to strictly ectodermal sense-organs. This, however, seems to lead us into serious difficulties, for, in the first-place, the terminal buds of the outer skin, which are very numerous in some fishes and which can hardly be other than ectodermal, are apparently all innervated from communis system. Again, the taste buds of the mouth of fishes all or nearly all lie in the region of the stomodæum and are therefore probably of ectodermal origin. These among other facts seem to forbid the employment, in the present state of our knowledge, of any such morphological criteria of the components as Johnston adduces. Indeed, the basis for the segregation of the components may be fundamentally physiological, as Cole and Kingsbury seem inclined to believe.

August 1, 1898.

#### REVIEW OF JOHNSTON ON THE CRANIAL NERVES OF THE STURGEON.<sup>1</sup>

By O. S. STRONG,

Columbia University.

This communication contains a résumé of the results of the author's investigation on the hind brain of *Acipenser rubicundus*, Le Seur. The investigations were made by means of the method of Golgi on the brains of fishes 25 to 40 cm. in length. Only a few of the most striking results will be noted here, leaving a more detailed review till the appearance of the final paper. The work is of a character much needed in this field at present and though surprising in some respects, the results will doubtless be very valuable.

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<sup>1</sup> Hind Brain and Cranial Nerves of *Acipenser*, by J. B. Johnston (University of Michigan). Anatomischer Anzeiger, XIV Band, Nr. 22 and 23, 1898.

The ventro-lateral tracts of the medulla appear to be made up of the neurites of commissural and tract cells, as has been described in the spinal cord of Selachians and Teleosts. The smaller number of the fibers of the fasciculus longitudinalis posterior come from the central diffuse nucleus of the thalamus, the greater number from the motor cells of the ventral horn along the course of the fasciculus in the medulla. Especially interesting is the statement that "it gives immediate origin to the VIth., to the larger part of the ventral root of the VIIth., to the whole of the ventral roots of the IXth. and Xth., and to the XIIth. nerve. A part of the ventral root of the VIIth., all of the ventral Vth., as well as the IVth. and IIIrd., arise from cells lying in the latero-dorsal portion of the ventral horn whose neurites pass more or less directly out into these roots without entering the fasciculus longitudinalis posterior."

A considerable part of the sensory portion of the trigeminus after it enters the medulla descends as the spinal V and principally terminates in an enlargement of the dorsal horn of the cord at the point of transition from cord to medulla (nucleus funiculi). The spinal V also receives contingents from the IX-X group as described by Strong and Kingsbury. The larger part of the fibers of the sensory Vth. (deep portion), however, enters the tuberculum acusticum where they form a distinct bundle running both forward and backward. The descending portion of the fibers of the Vth. entering the acusticum become arcuate fibers and most of them, possibly all, reach the opposite side of the medulla. This is a remarkable course for *direct* root fibers of the V, it may be remarked here, and should rest on a firm basis of observation. The ascending portion of the deep Vth., enters a nucleus at the anterior end of the medulla which is immediately continuous with the body of the cerebellum.

A part of the fibers of the VIIIth. end in relation to the Zwischenzellen of Goronowitsch, the remainder, together with the lateral line roots, also form ascending and descending bundles. One portion of the descending fibres (called the spinal VIIIth.) partly terminates in the nucleus funiculi and partly in a smaller nucleus mesad of it; the remainder of the descend-

ing fibers forms arcuate fibers like those of the deep Vth. The ascending fibers of part of the VIIIth. form a slender bundle close to the central cavity and terminate in relation to cells closely investing it. "The remainder of the VIIIth. fibers and all the ascending lateral line fibers run up to the cerebellum, most of them spreading out in the lateral lobes and the remainder entering the body." Some fibers of the ventral lateral line root of the VIIth. enter the so-called lobus trigemini which also receives the dorsal lateral line root of the VIIth. Owing to its entirely misleading character, Johnston proposes to substitute the name *lobus lineæ lateralis* for the term lobus trigemini. Its structure is similar to that of the tuberculum acusticum. In both are found three types of cells, (a) cells with short neurites like those in the cerebellum, (b) minute cells comparable with the granule cells of the cerebellum, and (c) a large number of cells comparable with the Purkinje cells. Kingsbury's view as to the non-identity of the lobus trigemini of Acipenser with the structure of the same name in Teleosts is confirmed.

The sensory fibers of the IX and X break up in the dorsal part of the lobus vagi. "These fibers end in relation with cells of the II type whose neurites break up mostly in the ventral and lateral parts of the lobe. This part of the lobe is made up of cells whose neurites take a ventro-lateral course to the lateral part of the medulla. Here the fibers either pass anteriorly or posteriorly without dividing, or they divide, one branch going anteriorly, the other posteriorly. The smaller number of fibers turn posteriorly. They form a distinct bundle of non-medulated fibers ventral to the spinal Vth. and continue into the cord. The anteriorly directed bundle runs ventral to the acusticum to the anterior end of the medulla, where it ends in a large nucleus, forming the antero-lateral limit of the medulla, lateral to the median Vth. nucleus. This is the Rindenknotten of Mayser and Goronowitsch." They are connected by a commissure.

The anterior part of the lobus vagi "which corresponds to the L. trigemini of Mayser is very much smaller in Acipen-

ser than in Teleosts and is composed chiefly of the root fibers of the dorsal VIIth." which enter it and turn caudad. Johnston very properly recommends that the name lobus trigemini be entirely dropped. It is amusing that all recent writers are agreed that the one nerve with which either species of "lobus trigemini" has nothing to do is the trigeminus.

The destination of the neurites of the Purkinje cells of the cerebellum was not determined but it is considered probable that they run through the acusticum to the base of the medulla. The fibers entering the cerebellum come chiefly from the medulla, the tectum and optic thalamus, also from the lobi inferiores. Johnston emphasizes the structural continuity of the cerebellum with the acusticum and is of the opinion that this fact points to the conclusion that the cerebellum is the enlarged anterior end of the center for the sensory nerves of the integument.

The facts above mentioned in connection with the cranial nerves lead Johnston to agree with Kingsbury in his analysis of the sensory centers in the main, but, in view of the partial mingling of the V-VIII-lateral line group in the medulla, to think that Kingsbury separates the spinal Vth. and the cerebellum from the acusticum more than is warrantable. On the other hand, Johnston emphasizes the distinction between the centers for the above group and the center—the lobus vagi—for the VII-IX-X group. After a brief consideration of the peripheral structures innervated by these nerves, he comes to the conclusion that "all sensory structures of ectodermal origin are supplied by components of the Vth. (including spinal Vth. components running in other nerves), VIIIth., and lateral line nerves, and that all fibers supplying such structures have their central endings in the nucleus funiculi, the tuberculum acusticum, or the cerebellum, except such as pass through the acusticum as arcuate fibers. On the other hand, all sensory structures of entodermal origin are supplied by VIIth., IXth. and Xth. components, and all fibers supplying such structures find their central endings in the lobus vagi."

In coming to this general conclusion the writer appears to have overlooked the important fact, which seems to be quite



certain, that fibers innervating end-buds scattered over the surface of the head and even the body of the Teleosts have their central termination in the lobus vagi. Such end-buds are of course ectodermal. The association of such fibers with visceral fibers is puzzling in any case and it has occurred to the writer of this review—as well as to C. Judson Herrick—that it might be accounted for on the supposition that the end-bud organs originated on or near endodermal surfaces. Such a supposition is, of course, merely speculative and unless it could be established, the fact that fibers innervating end-buds on ectodermal surfaces have their central termination in the lobus vagi would appear to constitute a fatal objection to Johnston's generalization that there are two distinct sensory systems—ectodermal and entodermal. The partial confusion of centers for the V-VIII-lateral line group which Johnston describes and which led him to group these nerves together, merits a careful consideration, however, by those who are attempting the analysis of the cranial nerves in fishes.

Johnston also comes to the conclusion that there appears to be "no structure in the cord with which the lobus vagi can be considered homologous." Consequently such nerves are not available in determining segments of the head homodynamous with trunk segments. He finally concludes that in using the cranial nerves to determine segmentation, it is probably best to disregard the sensory nerves altogether and use only the motor series.

The fibers of Meynert's bundle are traced beyond the ganglion interpedunculare. Most of the coarse fibers after decussating ventral to the ansiform commissure turn dorsad, pierce the above commissure and terminate in cells near the fasciculus longitudinalis posterior whose neurites cross the middle line in the ansiform commissure and join the ventro-lateral tracts. The fine fibers could not be traced with certainty, but there is reason to believe they terminate in a nucleus of small cells on the lateral surface of the lobus lineæ lateralis.

REVIEW OF ALLIS' PAPER ON THE CRANIAL NERVES OF AMIA.<sup>1</sup>

BY MISS CORNELIA M. CLAPP.

Mt. Holyoke College.

Mr. Allis seems now to have accomplished the task set for himself in 1886. This is the third paper which has appeared; the first being the admirable account of the "Anatomy and Development of the Lateral Line System of *Amia calva*;" the second, a short paper in '95, preliminary to the third which appeared about a year ago. It is, as it was intended to be, "an accumulation of facts and references grouped so as to be conveniently used as a basis for further work."

In the eighteen beautiful plates illustrating the paper, Mr. Nomura, the artist, has faithfully reproduced the dissections, many of which were made by himself.

The thoroughness of the work is indicated from the statement in the introduction, that "nothing is shown in the adult that was not controlled in larvæ, and everything found in larvæ has been sought for until found or accounted for in the adult." The chief merit of this voluminous paper lies in its accurate detail, making it invaluable to the anatomist as a reliable source of information.

From the study of the eye-muscles and their innervation, Allis thinks that the muscles of the eye in vertebrates are not homologous structures, the want of homology being found entirely in those muscles that are innervated by the oculomotorius and abducens, i. e. those muscles that are said to arise from van Wijhe's first and third somites. As the eye-muscles have been developed from the muscle masses in these two somites, different arrangements have arisen in the various groups of Ichthyopsida. On this basis Mr. Allis has constructed a number of prototypes, and has added another to the forest of genealogical trees.

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<sup>1</sup>The Cranial Muscles and Cranial and First Spinal Nerves in *Amia calva*, by Edward Phelps Allis. *Journ. of Morph.*, Vol. XII, No. 3, 1897.

Plate XXII shows the relation of the eye-muscles and the nerves innervating them, to the ophthalmicus profundus or nasociliaris trigemini. There are two main lines of descent: on the one hand, by the splitting of the large inferior oblique muscle, a new rectus internus is formed, the earlier muscle of that name disappearing or fusing with the rectus superior; this gives the condition seen in Petromyzon. On the other hand, the new muscle formed by the split becomes the rectus inferior and the earlier inferior rectus fuses with the rectus internus; thus arises the proto-urodele type, from which there are three lines of descent. One of these lines leads to the selachians, another to the fishes (ganoids and teleosts) and a third to the Amphibia and higher vertebrates. The amphibian branch shows two diverging lines of development, the one leading to Urodeles and the other to Anura, where a new rectus internus is formed and the old one disappears or is fused.

Allis remarks in general that "the lines leading to the higher types of each class resemble each other in that the superior branch of the oculomotorius in such lines innervates but *one of the muscles of the eye*, while in the lines leading to the lower types it always innervates *two*." He also says: "There has been but *one impulse*, if it may be so called, leading to the formation of the arrangements found in higher types and not repeated ones." We may suppose that the splitting of the large inferior oblique muscle spoken of above, is that impulse.

Allis states that this ancestral tree of the muscles and nerves of the eye-ball are based on "insufficient and perhaps inaccurate data," but it is interesting to note that the same grouping of orders of Ichthyopsida is shown by Hasse and Maurer; the former basing his conclusions on the study of the development and structure of the vertebral column and the latter on the development of the muscle cells and muscle fibers.

The innervation of sense organs is discussed at length in this paper, and much of the "review and comparison of nerves" has great interest for those working along these lines.

Since '88 Allis has discovered that the glossopharyngeal nerve takes no part in the innervation of the canal organs, the

so-called dorsal root of that nerve receiving its fibers from the root of nervus lineæ lateralis and from the ramulus ampullæ posterioris.

If the terminal buds, found in such numbers and so irregularly distributed over the head of *Amia*, represent a stage in the development of the canal organs, they and the nerves innervating them should arise in connection with sensory ectodermal thickenings, as do the canal organs and their nerves. Allis has shown that those trigeminal and facial nerves, in *Amia*, that are known to innervate terminal buds or regions where those buds abound, all arise from the median, fasciculus communis portion of the main trigemino-facial ganglion. He thinks it probable, as Strong has suggested, that "the fasciculus communis tract of the brain is largely or entirely concerned in the innervation of terminal buds."

The chorda tympani belongs probably to the fasciculus communis nerves, and is represented in *Amia*, by the mandibularis internus trigemini.

There is no true ramus ophthalmicus profundus in *Amia*, but the ganglion is distinct, and a rudiment of the nerve is sometimes seen.

The "hitherto undescribed cranial nerve" of Pinkus in *Protopterus* is found in *Amia*.

## THE GIANT GANGLION CELL APPARATUS.

By ULRIC DAHLGREN,

Princeton University.

The following report, read before the Neurological Seminar of the Marine Biological Laboratory in July, 1898, is an outline of some recent work on the problem presented by the "Giant Ganglion Cells" found in the median dorsal fissure of the myelon of a number of fishes. This report includes several recent advances made by the writer on the problem in question.



The name "Giant Ganglion Cells" is objectionable, as it not only describes nothing but their size, but is used for other large nerve cells in many scattered forms of the invertebrate animals as well as the vertebrates. "Median Cells" or "Dorsal Cells" would seem better, but the writer will refrain from committing himself to a new term until more is discovered concerning the apparatus.

These cells were first described in *Lophius piscatorius* by Fritsch. In this fish they number about 200, are very large and are massed in the anterior portion of the dorsal median fissure. Each one gives rise to a single large neurite, according to Fritsch, which dips down into the cord and becomes a constituent fiber of one or the other of two lateral, symmetrical fiber-bundles. The fibers thus forming part of these bundles pass *cephalad* into the brain and out of that through certain roots of the 10th and 5th nerves. Fritsch considers them to be sensory nerves.

Tagliani found the same large cells in a similar position in the myelon of *Balistis* and of *Orthogoriscus*, in which latter animal he found the fibers running both *cephalad* and *caudad*.

In my article of 1896 (*Anat. Anz.*, Bd. XIII, p. 281) I described these giant cells in a large number of *Heterosomata*, or flounders, and found that the neurites entered the usual fiber-bundles but ran *caudad* in them instead of *cephalad* as Fritsch described for *Lophius*. At the same time I gave certain reasons for believing that this apparent difference in neurite-distribution did not prohibit the homology of the cells in the different forms (p. 291). Other and more satisfactory proof that the giant cells of these fishes are homologous has been found since and consists of the following facts. The giant cell apparatus of *Pseudopleuronectes Am.* was further studied by means of Palladino's Palladium Iodide method (Lee, IVth Ed., p. 413) by means of which it was possible to trace the neurites with more ease and certainty than before. It was then found that in many of the cells the large neurite bifurcated just before entering the fiber-bundle and one branch ran *cephalad*, while the other ran *caudad*, both in the bundle. A Pediculate fish, nearly allied to

*Lophius* was then examined and the missing caudal fiber was immediately discovered. This fish, *Pterophryne histrio* possesses only 24 giant cells which is the smallest number yet found in an adult teleost fish. These cells are very large and closely resemble those of *Lophius* in every particular. Having demonstrated this bifurcation of the giant cell neurite in these two forms, it is probable that the same will be found to hold true for the other fishes possessing this apparatus.

The number of species in which the giant cell apparatus appears, has been found to be far greater than supposed. A vast number of teleost fishes possess it and the writer does not hesitate to estimate that this number is over one half of the living species. It is found less frequently in the lower orders, the NEMATOGNATHI, for instance, not showing one instance as yet in which it has been found; while the PEDICULATI and HETEROSOMATA fail to yield one species which does not possess it in a highly differentiated and developed form. Where found in a more primitive form it is characterized by the large number, small size, and simple structure of its ganglion cells, while in the specialized forms the ganglion cells are fewer and of monstrous proportions and uncouth structure.

Its relation to the "Transient Ganglion Cells" or "Transient Nerve Apparatus," described in *Salmo*, *Raja*, etc. by Rohon, Beard, Van Gehuchten and others, is clearly, in the writer's mind, one of identity; the giant cell apparatus being composed of some or all of the transient cells which have remained.

Van Gehuchten's discovery of the bifurcation of the neurite of the transient ganglion cells of *Salmo* must therefore be considered the first exposition of this fact for the giant cell apparatus as well.

Many embryonic fishes have been found to possess the transient apparatus and the writer doubts if any form of teleost is without it. Work will be continued on *Pseudopleuronectes Am.* and other forms.

## INNERVATION OF THE OLFACTORY EPITHELIUM.

By A. D. MORRILL.

Hamilton College.

The innervation of the olfactory organ is of interest as it is the only sense organ, in vertebrates, where continuity of the nerve-fibers with the sensory cells exists, according to the large majority of investigators.

The statement by Dr. Ayers that the relation of the nerve fibers to the sensory cells was the same in the cochlea of the pig as in the olfactory organ of vertebrates led me, after studying the relation of the fibers and sensory cells in the ampullæ of the ear of the smooth dog-fish, to try the same methods with the olfactory organ of this fish.

In the ampullæ, with Ehrlich's method, I found contact and free endings but no case which seemed to be true continuity. In the olfactory organ I found continuity and some free endings but nothing that resembled the relations found in the ampullæ.

I found the three types of cells described by Dogiel in his paper on the olfactory epithelium of the sturgeon: 1st, spindle-shaped; 2nd, cylindrical with a slight constriction near the middle; 3rd, conical, cells. All are ciliated and continuous with nerve fibers, which extend toward the brain. Between these olfactory cells are long irregular shaped supporting cells. Whether the difference in shape of the sensory cells is due to difference of function or to mechanical causes was not determined.

The development of the olfactory nerve and epithelium have been much studied in connection with the problem of metamerism in the vertebrate head. Some investigators, with Marshall, consider the olfactory nerve as the first cranial and consequently of segmental value, while others regard it as similar to the eye in being a modified portion of the brain.

The recent paper of Disse on the development of the olfactory nerve and epithelium in the chick is of considerable in

terest on this account. He found, with the Golgi method, in the olfactory pit of the third day chick neuroblasts with tapering processes pointing toward the central portion of the epithelium but found no trace of a nerve. Supporting cells were found between the neuroblasts (Fig. 1). This had been observed by His and others.

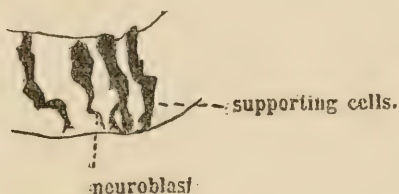


Fig. 1. After Disse.

At the fifth day the nerve processes from the neuroblasts were found to have extended quite a distance from the epithelium toward the brain but had not reached it. During the sixth day the fibers were found penetrating the outer portion of the brain which was still free from cells and the processes easily followed as had been previously observed (Fig. 3).

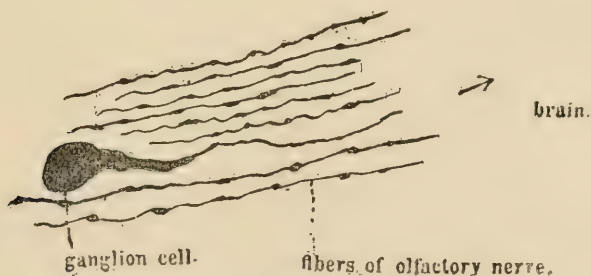


Fig. 2. After Disse.

The ganglion cells found quite early in the developing olfactory nerve between the fibers and considered by His as bipolar Disse claims to be unipolar and since he finds them first in that part near the olfactory epithelium and of the same shape as the neuroblasts and later finds them nearer the brain which



they finally enter and since only one process was ever observed and that on the side toward the brain, he concludes that some of the neuroblasts have migrated into the nerve and finally reach the brain (Fig. 2).

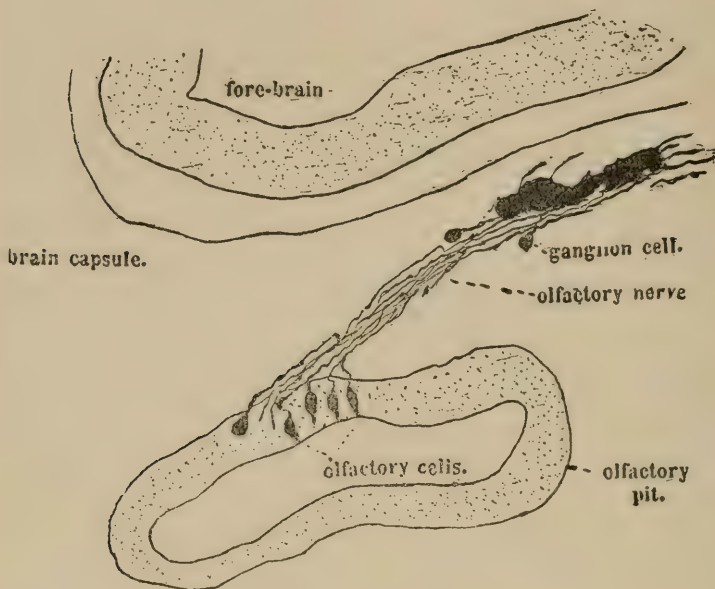


Fig. 3. After Disse.

His found cells which he described as bipolar in the developing nerve and on this account thought that the term olfactory ganglion was more appropriate than olfactory nerve.

The main points claimed by Disse are: 1st, confirming previous investigators that the olfactory nerve develops from neuroblasts in the olfactory epithelium; 2nd, That a part of the neuroblasts wander into the olfactory nerve and pass eventually into the brain but remain unipolar; 3rd, He considers the olfactory nerve as embryonic in character with cells of origin remaining in the olfactory epithelium. The fibers are non-medullated and in these respects quite different from the cranial nerves.

## THE GIANT GANGLION CELLS IN THE SPINAL CORD OF CTENOLABRUS ADSPERSUS (WALB.-GOODE).

By PORTER E. SARGENT,  
Harvard University.

During the winter of '97-'98 while engaged in the study of Golgi preparations of the central nervous system of the common cunner, *Ctenolabrus adpersus*, my attention was attracted to large bodies lying in the median dorsal fissure of the spinal cord. A little study showed them to be nerve cells of gigantic proportions, giving off a ventral process.

The following preliminary paper is a summary of studies made during the spring of 1898. No attempt at a critical discussion of the subject will be attempted in this paper, that being reserved for the final article. I wish here to express my obligations to Prof. E. L. Mark for kindly advice and assistance, and to Mr. Alexander Agassiz for opportunities enjoyed at his Newport Laboratory, where the material for this study was collected and prepared.

Colossal ganglion cells in the spinal cord of certain Ichthyopsida have attracted the attention of a large number of observers during the past forty years. Upward of sixty articles in the literature deal with the subject to a greater or less extent. The greater number of these papers have to do with a transient nervous apparatus existing only in the embryos and larval stages. The most recent papers on this subject are those of Studnicka '95 and Beard '96.

In adult fishes giant ganglion cells occurring in the dorsal portion of the cord have been noted by many investigators from Müller '44 to Kolster '98. Most of these observations are fragmentary and all are very incomplete, so that as yet little is known of the occurrence, distribution and structure of these cells, and almost nothing of the course of their fibers, while their function is a mere matter of conjecture. In only one instance have the neurites been traced. Fritsch '84 and '86 found that the giant cells imbedded in the anterior part of the cord of

Lophius, sent their axis cylinders cephalad to the roots of the Trigemini and Vagus nerves.

Three recent papers bearing more directly on this subject deserve notice here. Dahlgren '97 finds in the embryos and adults of the order Heterosomata certain giant ganglion cells lying in the median dorsal fissure or in a double row on either side of the dorsal fissure of the cord, and varying in number from 69 to 500 in different species. These cells give off neurites all of which run caudad in two fiber bundles lying bilaterally in the dorsal part of the cord. The neurites were followed but a short distance through the bundle, and their termination was not made out. The suggestion is made that they are connected with sense organs in the fins. Kolster '98 describes giant ganglion cells lying in the dorsal fissure of the cord of *Perca fluviatilis*. The cells are stated to have no dendrites and the neurites were followed but a short distance, the direction which they take not being stated. The hypothesis is advanced that they have the function of raising the spines of the dorsal fin. Tagliani '97 has described the occurrence of similar cells in *Orthogoriscus* and *Tetrodon*.

There has been a tendency among writers on this subject to consider as homologous all the colossal ganglion cells occurring in the dorsal part of the cord in the various groups of Ichthyopsida, or to make wide and sweeping generalizations as to their homology, although at the same time the greatest diversity of function has been hypothetically ascribed to them. A comparison of the very diverse conditions described in various fishes and the utter lack of harmony in the homologies made by different writers, taken in connection with my own observations on many different species, justifies the conclusion that the conditions are much more diverse and complex than has yet been recognized, and that these varied elements are not homologous throughout the Ichthyopsida, or even throughout the group of fishes. Though they may have had a common origin in the ancestral giant cells of worms and crustaceans, they have assumed such very different form, position and function that they cannot be said to be homologous; and it is perhaps more

probable that they have been independently derived from less conspicuous elements as the occasion for great size has arisen.

*Methods.*—The brain and spinal cord was carefully removed and immediately fixed in one of the following fluids,—

- (1) 10% solution of Formol.
- (2) Saturated aqueous solution of Corrosive Sublimate.
- (3) Flemming's stronger chromic-osmic-acetic fluid.
- (4) Potassic Bichromate, gradually raised from 2% to 5% solution.

Many stains fail to bring out clearly the giant cells and their neurites though staining other parts of the nervous system well. This is particularly true of the carmine stains. The following in the order named proved the most valuable:

1. Kenyon's Copper Sulphate Phosphomolybdic Acid Hematoxylin, following formol preservation.
2. Heidenhein's Iron Hematoxylin, used on formol or sublimate material.
3. Sahli's Methylene Blue Acid Fuchsin Axiscylinder Stain, used on Bichromate material.
4. Ehrlich's Acetic Acid Alum Hematoxylin double stained with Congo red, or Acid-fuchsin.

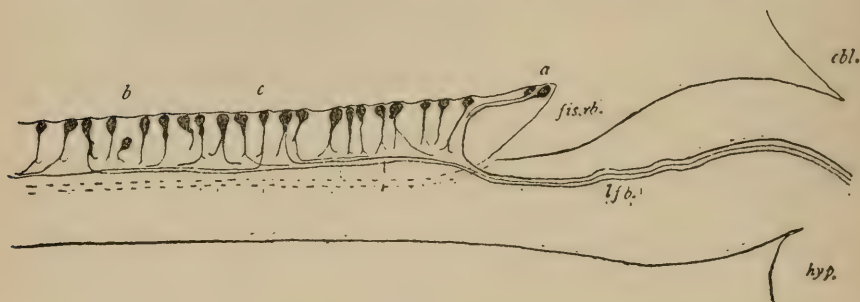
The first stain proved of the greatest value, and as this is the first time, I believe, that it has been used on vertebrate material, deserves a word of comment. Material fixed in 10% formol and preserved in 5% was washed and put in a 5% solution of copper sulphate for 24 hours, by which time it had assumed a green color. After cutting in paraffin and mounting in the usual way, they were stained on the slide from 15 to 30 minutes, in the following:—

10% Phosphomolybdic acid,	.	1 c.c.
Hematoxylin crystals,	.	1 gm.
Chloral hydrate,	.	10 gms.
Water,	.	400 c.c.

They were then rinsed in water, dehydrated, cleared and mounted in the usual way. This is an excellent differential stain for neuroglia, the dendrites of ganglionic cells and especially the axis cylinders, the myelin being left wholly unstained.



The giant ganglion cells of *Ctenolabrus* form a single median longitudinal row in the dorsal portion of the cord, lying within the dorsal fissure with their upper surfaces flush with the dorsal limit of the cord, and covered by the membrana prima, (fig. 3). Each cell lies within a capsule formed of three elements,—(1) the membrana prima which is arched above each cell, (fig. 5, *mb.* p. 190), (2) the neuroglia fibers (*n.f.*), which



*Fig. 1*.—Diagrammatic parasagittal section of the medulla and anterior part of the cord of *Ctenolabrus*, showing the arrangement of the giant ganglion cells and the course of their neurites. The lateral bundle (*l.f.b.*) and the lateral cells (*a*) are projected on the median plane. The canalis centralis is shown in dotted lines. *fis.rb.* fissura rhomboidalis ; *cbl.* cerebellum ; *hyp.* hypoaria.



*Fig. 2*.—Diagrammatic frontal section of same, the cells and lateral fiber bundles projected on a plane. *Opt. l.* optic lobe.

come off from the membrana prima and extend downward to the canalis centralis, (3) the fine neuroglia network, (*n.n.*). The capsules have an internal diameter of one and a half to two times that of the cell, so that each cell is surrounded by a space,

in which it is partly supported by the numerous dendrites which run off from the cell to the surrounding neuroglia.

The giant cells extend from the posterior end of the fissura rhomboidalis caudad through the anterior end of the cord, (fig. 1). The largest cells are toward the anterior end of the series, and there is some diminution in size posteriorly. They are as a rule more closely set anteriorly, being separated from each other by intervals of from one-fourth to one-half their diameter. The intervals between the adjacent cells increases posteriorly to three and four times the diameter of the cells, the last few being irregularly placed at perhaps greater intervals (figs. 1 and 2). The cells tend to become aggregated in groups of three or four, separated from other groups by wider intervals. In the anterior portion of the series mutual crowding may influence the form of the cells, or may result in pushing some of the cells to one side of the median line, or downward below the level of the others. Occasionally two cells may be found in a transverse section lying side by side.

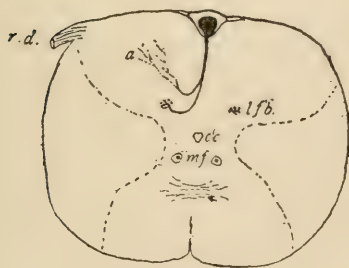


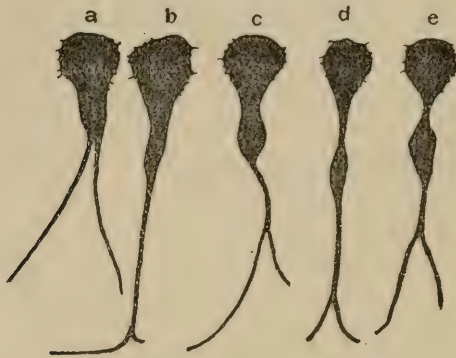
Fig. 3. Diagrammatic transverse section of the anterior part of the cord. The outlines of the grey matter are shown in dotted lines. *r.d.* radix dorsalis; *c.c.* canalis centralis; *m.f.* Mauthner's fibers.

On either side of that portion of the canalis centralis where it widens out and opens into the fissura rhomboidialis there are similar cells bilaterally placed, usually two on each side but the number may vary from one to three (fig. 2, *a*). In fig. 1, these are shown projected upon the median plane (*a*). Rarely similar giant cells are found which do not lie in the dorsal fissure but lie laterally, deeply buried in the cord, (fig. 1, *b*).

This condition occurs in about one case out of 300.

*Size.*—In the youngest fishes 3 cm. in length the cells have an average diameter of 7 or 8  $\mu$ . In the various stages

from the half grown individual 10 cm. long, to the full grown fish of 20 cm. there is a difference in the size of the cells keeping pace with the growth of the body. In the adult there is considerable variation in the size of the cells. The smaller having a minimum diameter of  $40\ \mu$ , the larger of  $70\ \mu$ , with an extreme length to the beginning of the axis cylinder of  $150\ \mu$ . The number of cells in a single fish is between 35 and 40, and seems to be fairly constant regardless to the age or size of the fish.



*Fig. 4.* Five Giant Ganglion Cells showing variation in form and branching of the neurites.

The form of these giant cells, though always characteristic, is very variable. In young specimens of *Ctenolabrus* 3 cm. in length the cells show much greater regularity in form and distribution than in the adult. In the anterior part of the cord they lie closely together, the intervals increasing regularly posteriorly. The cells are usually rounded, but anteriorly mutual pressure may give them a somewhat angular outline. Occasionally in the smallest specimens examined, the cells are uniformly dorso-ventrally flattened, approaching a discoid or lenticular form.

In the adult the simplest form is approximately spherical (Fig. 5), but this form grades off to the pyriform which is the most typical (Fig. 1 *c*, Fig. 4 *b*). The tapering end is ventral and from it comes off the axis-cylinder. This may pass off

from the cell abruptly as the stem from a pear, or the cell may gradually taper out into the axis-cylinder. In their variation in form the cells may approach the oval, the conical, the discoid, club-shape, or they may be irregular. One interesting variation in form assumed is shown in Fig. 4 *e*, where the cell is apparently drawn out into two parts. Every gradation may be observed from the gradually tapering cell (*b*) through forms like *d* and *c*, to the apparently double cell *e*.

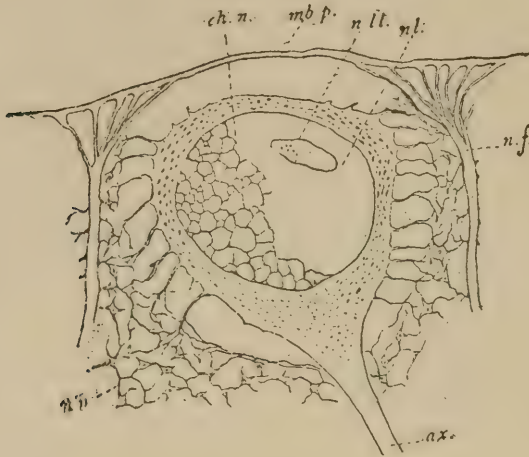
Numerous dendrites are given off from the cells, varying from the finest filaments to processes of considerable size. They are given off most freely from the dorsal part of the cell, and as a rule do not greatly influence the outline, but particularly in the anterior bilaterally placed cells they are occasionally so large as to give the cell a multipolar appearance. These dendrites branching freely pass through the open space of the capsule surrounding the cell (Fig. 5), and interlace and anastomose with the surrounding neuroglia cells, forming thus a direct protoplasmic connection between the giant ganglion cell and the neuroglia. In some few cases observed there is apparently a direct anastomosis of the dendrites of the adjacent ganglion cells.

*Nucleus*.—The internal structure of the cell is peculiar and characteristic. The nucleus is abnormally large nearly filling the cell and having in general much the same outline as the cell itself (Fig. 5). The nucleus is eccentrically placed usually crowded close up to the dorsal wall of the cell so that occasionally the cytoplasm can with difficulty be distinguished between the nucleus and the cell wall at that point. The chromatin network can be seen distinctly in iron hematoxylin, and Ehrlich's hematoxylin preparations, extending uniformly through the cell, (Fig. 5, *ch. n*).

The nucleolus is large, oval or spheroidal, usually lying eccentrically in the upper part of the nucleus. (Fig. 5, *nll*). It takes most stains deeply, but nuclear stains like Ehrlich's hematoxylin leave it transparent. Rarely a second nucleolus of smaller size may be seen. The nucleolus contains from eight to twelve spherical granules which stain deeply with iron



hematoxylin, but remain transparent and highly refractive in preparations double stained with Ehrlich's hematoxylin and Congo red.



*Fig. 5.* Diagram of Giant Ganglion Cell and its surrounding capsule. *nl.*, nucleus; *nll.*, nucleolus; *ch.n.*, chromatin network partly drawn in; *mb.p.*, membrana prima, *n.f.*, neuroglia fibre; *n.n.*, neuroglia net; *ax.*, axis cylinder.

Immediately around the nucleolus the karyoplasm often stains less deeply than in its more peripheral parts. This may be attributed to the karyoplasm in that region being greatly vacuolated. This lightly staining region varies greatly in size, and the definiteness of its outline. The chromatin net showing faintly may be followed from the lighter area to the darker area showing the continuity of the karyoplasm. Usually this area is relatively small and its limits indistinct, the denser karyoplasm gradually becoming lighter toward the nucleolus. Sometimes it is entirely absent, karyoplasm being homogeneous throughout. This lighter area is often of peculiar and varied shape, sometimes crescentic occasionally sending out forked tongues toward the periphery of the nucleus. In some preparations what corresponds to this area is an empty space, and the karyoplasm can be seen to have shrunk away from the nucleolus at one side leaving a crescent-shaped space.

From the examination of a single cell of this kind a quite different interpretation would be possible, namely that the lighter area is the nucleus and the darker substance a differentiated cytoplasm aggregated about the nucleus. The examination of several hundred cells preserved and stained by a variety of methods shows that this is not the case.

The cytoplasm has the characteristic shining appearance of a highly refractive substance. Under a 1-12 in. oil immersion it shows a finely granular structure. The chromophilic granules are elongated and lie with their long axes parallel and concentric with the cell wall (Fig. 5). They are most conspicuous in the dorsal and larger end of the cell, gradually fading out toward the point from which the axis cylinder comes off. The cytoplasm lies principally in the lower part of the cell, but usually may be seen to extend around the periphery of the cell. In cells having the form of those in Fig. 4 the nucleus is approximately spherical and lies in the upper part of the cell, the cytoplasm having the appearance of having been crowded downward.

*Neurites*.—As has already been stated, the cells are in general unipolar giving off a large neurite which passes ventrally into the cord (Fig. 3). The course of the neurite may be directly ventrad, or obliquely inclined cephalad or caudad, or again it may run horizontally near the surface for a distance of five or six diameters of the cell before passing downward into the cord. Rarely a neurite is seen to pass out laterally from the cell and become lost in the grey substance. The neurites of anterior bilaterally placed cells run caudad near the surface of the cord for some distance, then curving ventrad, laterad, and cephalad pass forward through the fiber bundle. The neurite having passed down one-half or two-thirds the distance to the canalis centralis curves gradually either to the right or left, sometimes dividing and finally enters or sends one of the two branches into the lateral bundle made up of similar fibers. The neurites pass alternately to the right or left, but this does not

hold strictly, sometimes several successive cells sending their neurites to the same side.

Entering the lateral bundle the neurite may pass either cephalad or caudad (Figs. 1 and 2). Dahlgren '97 finds that in the order Heterosomata the neurites *all* run caudad. In examining upward of three hundred cells in which the neurites were followed into the bundle, approximately one-third were found to send the neurite through the bundle caudad, the other two-thirds cephalad. This harmonizes with results obtained by counting the number of fibers in the bundle at different parts of its course, which shows that the majority of the neurites run cephalad.

In approximately two-thirds of the number of cells examined the neurite was found to divide into axis cylinders of equal diameter. In the other one-third no such branching could be seen. This may sometimes have been due to the imperfection of the preparations, but in a few instances at least it would seem that the neurites do not divide.

There is a remarkable and interesting variation in the manner of this division. In the most common type (Fig. 4 *b*) the neurite passes ventrad and laterad nearly to the level of the bundle and then splits into two equal axis cylinders at least one of which enters the bundle and passes through its entire course. The division may take place higher up near to the cell, the two branches diverging as they pass downward (Fig. 4, *c* and *e*). Or the division may occur so high up that the two processes come directly from the cell (Fig. 4, *a*). In a few cases the division was observed to take place after the neurite had entered the bundle, the two resulting processes continuing parallel for some distance.

The axis cylinder stains deeply with iron hematoxylin, Kenyon's or Sahl's method, and is uniformly stained throughout its length. Frequently however the initial part of the fiber immediately adjacent to the cell takes the stain but lightly, the protoplasm of that part of the neurite staining precisely like the cytoplasm of the cell, with which it seems to be continuous and identical. The axis cylinders are throughout their course

unmedullated, but Schwann's sheath is present showing the characteristic nuclei.

The neurites form two distinct and characteristic fiber bundles lying symmetrically on either side of the cord lateral and dorsal to the canalis centralis (Fig. 3, *l. f. b.*) They may be distinguished throughout their course from other adjacent fibers by three characteristics, (1) the absence of a medullary sheath; (2) their large size; (3) their aggregation into a characteristic bundle. Each bundle in the region of the medulla consists of from nine to twelve fibers. At the posterior limit of the series of giant cells in the cord the bundles consist of four or five fibers. The number increases cephalad of this point as the neurites enter the bundles.

In their course through the cord the fibers lie within the dorsal horn of the grey substance close to its lower limit. The fibers here are loosely aggregated having a somewhat undulating course. In the medulla the bundles rise to the level of the floor of the fourth ventricle, and at the same time curve laterad. Forward of this they again become depressed. In the medulla the fibers are closely pressed together, so that in cross section each fiber has a more or less sharply polygonal outline. In the medulla the bundles are often abruptly deviated from their direct path in passing around the deep roots of the cranial nerves. In the region of the fifth cranial nerve the fiber bundles curve laterad and ventrad and pass out through the ventral root of this nerve. The fibers have been traced out *into* the nerve, and have been traced through their course in a considerable number of series cut in the frontal, sagittal and transverse planes.

The course and ending of the fiber bundles posteriorly yet remains to be worked out. That branch of the neurite which does not enter the lateral bundle is difficult to follow, owing in part to the peculiar filiform neuroglia structures in that part of the cord, which strongly resemble the non-medullated fiber of the giant ganglion cells. The evidence derived from the study of many preparations indicates that this branch turns laterad



and dorsad and branching finely becomes lost in the network of the dorsal horn of the grey substance (Fig. 3, *a*).

#### SUMMARY.

In the anterior third of the spinal cord of *Ctenolabrus* there is a series of from 35 to 40 giant cells lying in the dorsal fissure, each cell within a capsule.

At the anterior end of this series and near the posterior edge of the *fissura rhomboidalis* there are two pairs of giant cells lying bilaterally near the surface of the cord.

The form of the cells is variable. Numerous dendrites are given off which anastomose with the surrounding neuroglia cells.

The cytoplasm contains elongated chromophylic granules arranged concentrically with the wall of the cell.

Each cell gives off an axis cylinder which runs ventrad and laterad usually dividing into two neurites of equal size, one of which enters the lateral fiber bundle.

This neurite follows the fiber bundle through the cord either cephalad or caudad.

The fiber bundles passing forward through the cord and medulla pass out through the ventral root of the Trigeminal nerve.

The other branch apparently divides and becomes lost in the network of the dorsal horn.

ON VARIATIONS IN THE DISTRIBUTION OF THE SPINAL NERVES  
ENTERING THE LUMBAR PLEXUS.

By C. R. BARDEEN,

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Special attention has been given during the last two or three years in the Anatomical Department of the Johns Hopkins University to the origin and distribution of the main nerve trunks in the human body. The students in practical anatomy have been encouraged to note carefully any variations from the usual descriptions of the courses of the various nerves and to record the results of their observations on printed "tabulation charts" furnished them. Besides the filling in of the printed charts, diagrammatic drawings have been freely made as a further means of illustration. The work has been verified and the charts have been carefully controlled by Dr. A. W. Elting during the early part of the undertaking, during the sessions of 1896-1897, and by myself during the past year.

In these records sex, color, apparent age, and marked peculiarities of bodily structure have been carefully noted as well as the distribution of the larger nerves. It is hoped that from these charts interesting and valuable statistics relating to the distribution of the peripheral nerves may be obtained. There is a very great variety in the modes of origin and distribution of the peripheral nerve trunks in certain regions of the body. This is well illustrated by the conditions found in the nerves entering into and leaving the lumbar plexus. To a consideration of these nerves I invite your attention to-day.

In man the lumbar plexus is formed as follows:

The eleventh thoracic nerve has in the main the characteristics of a typical segmental nerve. It divides into a dorsal primary division for the supply of the skin and muscles of the back and a primary ventral division for the supply of the ventro-lateral musculature and skin, and gives off a visceral branch,

or branches, which enter the sympathetic system. The ventral division has two main branches, a lateral, piercing the muscles at the side and giving off dorsal and ventral branches, and a ventral, extending well towards the median line in front, running for the most part between the muscles, but finally piercing them and supplying the skin in front. This ventral branch of the eleventh nerve usually becomes sub-cutaneous in a region somewhat below the umbilicus. It usually anastomoses freely with similar branches from the tenth and twelfth nerves.

In addition, the primary ventral division of the eleventh nerve may give off near the spinal column a branch of communication to the corresponding branch of the twelfth thoracic nerve.

The twelfth thoracic nerve likewise has the characteristics of a segmental nerve, supplying the region immediately caudal to that supplied by the eleventh nerve. The lateral branch usually extends well down over the middle third of the iliac crest. In addition to the ventro-lateral nerve, or in place thereof, the ventral division may give rise, usually near the spinal column, to the *ileo-hypogastric* nerve. This nerve runs to the ventral third of the iliac crest, there divides and sends an *iliac* branch over the lateral hip region and a *hypogastric* branch to the abdomen just above the pubis. This nerve bears varied and often very intimate relations to the ventro-lateral nerves. More rarely origin is given to the *ileo-inguinal* nerve. This nerve has a course very similar to that of the ileo-hypogastric but supplies a more ventral region of the hip, and the skin of the pubic region and root of the penis and of the scrotum and the adjacent part of the thigh. There are often anastomoses between the ileo-inguinal and the ileo-hypogastric nerves. The iliac branch of the former is often wanting.

The first lumbar nerve has no true ventro-lateral branch. Its place is usually supplied by the ileo-hypogastric and ileo-inguinal nerves which have many of the characteristics of ventro-lateral nerves. In addition, the first lumbar usually gives rise to the *genito-crural* nerve or to one of its branches. This nerve, sometimes with separate genital and crural branches, runs

down through the psoas muscle and across to the pubis. The *crural* branch supplies the skin of the upper leg just below Poupart's ligament, the *genital* branch passing down the inguinal canal and anastomosing with the inguinal nerve supplies a region similar to that innervated by the latter. The extent of distribution of the genital is inversely proportional to that of the inguinal.

There is usually a branch of communication from the ventral primary division of the twelfth thoracic nerve to that of the first lumbar. A similar branch from the first lumbar to the second is even more constant. There may be a similar connection between the second and third and between the third and fourth lumbar nerves. There is thus a sort of "collector" nerve formed which may run from the eleventh thoracic to the fourth lumbar nerve. So long a course however is rare. Indeed it is doubtful if nerve fibers often pass thus over more than two segments. Certainly the majority usually enter the nerves arising from the segment immediately below.

From this "collector" nerve and from branches springing directly from the second, third, fourth and rarely the fifth lumbar nerves arise the *obturator* and the *anterior crural* nerves.

The obturator arises from the ventral surfaces of these nerves. Passing through the obturator foramen it supplies the adductor muscles of the leg and some of the skin of the inner thigh.

The anterior crural nerve arises mainly from the dorsal surfaces of the spinal nerves and passing over the iliac crest supplies the extensor muscles of the thigh and the skin of the outer, middle and inner ventral regions of the upper leg and of the inner side of the lower leg. The nerve supplying the outer side of the thigh (the external cutaneous) usually arises separately from the main trunk; the other cutaneous nerves of the thigh may do so. Sometimes an "accessory obturator" runs over the pubic crest to supply the pectineus muscle and anastomose with the obturator.



The variation in the relation of these different nerves to the spinal nerves is expressed in the following tables:<sup>1</sup>

TABLE OF DISTRIBUTION OF SPINAL NERVES.

This table gives a summary of the distribution of the ventral primary divisions of the various spinal nerves entering the lumbar plexus. "Comm. br." indicates a proximal communicating branch between the given spinal nerve and the next below. The percentage sign refers to the ratio of the number of the plexuses in which the given condition is found to the total number of plexuses (122). The names of the various peripheral nerves indicate *direct* origin from the given spinal nerve. "Types of distribution" refers to the various distinct modes by which the constituent elements of the spinal nerve have been found distributed.

*11th Thoracic.*

Comm. br. each side.....	1	body
" " one side only.....	4	bodies
" " total.....	4.9%	
Types of distribution.....	4	

*12th Thoracic.*

Comm. branch.....	54.9%
Ileo-hypogastric.....	41.7%
Both.....	25.4%
Ileo-inguinal.....	5.7%
Types of distribution.....	9

*13th Thoracic.*

Found in one body.	
Comm. br. on one side.	
Ileo-hypogastric on each side.	
Ileo-inguinal on one side.	

*1st Lumbar.*

Comm. branch.....	85	%
Ileo-inguinal.....	86	%
Ileo-hypogastric.....	60	%
Ileo-hypog., no comm. 12d	27.8	%
Genito-crural.....	47.5	%
Types of distribution.....	26	

*2d Lumbar.*

Comm. branch.....	53.2%
Genito-crural.....	72.9%
External cutaneous.....	54.9%
Anterior crural.....	46.7%
Obturator.....	39.3%
Types of distribution.....	50

*3d Lumbar.*

Anterior crural.....	100	%
Obturator.....	100	%
Accessory obturator.....	5.7	%
Types of distribution.....	12	

*4th Lumbar.*

Comm. br. sacral plexus....	93.4%
Anterior crural.....	98.4%
Obturator.....	96.8%
Accessory obturator.....	5.7%
Types of distribution.....	7

*5th Lumbar.*

Anterior crural each side...	2	bodies
" " 1 side only.....	5	
Anterior crural, total.....	7.4%	
Obturator each side.....	1	body
" " 1 side only.....	6	bodies
Obturator, total.....	6.5%	
5th lumbar in lumbar plexus	8	bodies

<sup>1</sup> These statistics are based upon a study of but a part of the tabulation charts. They are based upon the conditions found in sixty-one bodies, or 122 lumbar plexuses. It is probable that when all of the charts have been examined the figures given will need some alteration, as expressive of the lumbar plexus. The tables, extended so as to include tabulations from a greater number of charts, will appear in a more extended article on the lumbo-sacral plexus, in the preparation of which Dr. A. W. Elting and myself are at present engaged.

The most notable thing brought out in this table is the great variety in the distribution of those spinal nerves which supply the cutaneous nerves distributed to the regions where the thigh and abdomen meet.

There is nothing especially remarkable about the distribution of the eleventh thoracic nerve. It is interesting to note however that in one of the cases in which there was a communication between the eleventh and twelfth thoracic nerves, a thirteenth thoracic nerve was found. It is to be noted that the ileo-hypogastric nerve arises in over 40% of the plexuses directly from the twelfth thoracic. In the text-books it is said to arise from the first lumbar nerve. The first lumbar nerve is essentially the source of supply of the ileo-inguinal nerve. In a little over 25% of the specimens it alone gives rise to the ileo-hypogastric. It is intimately connected with the genito-crural and seems to be the main source of cutaneous supply to the border-land between the thigh, the genitalia and the abdomen.

While the main strength of the second lumbar is given to the obturator and the anterior crural nerves, either directly or through the communicating branch, it also contributes largely to the external cutaneous, and to the genito-crural. The great variety of the paths by which this nerve is distributed is remarkable. Of the third lumbar nothing special need be said. The fourth lumbar as a rule is divided between the two great nerves of the lumbar plexus, and the sacral plexus. In thirteen per cent. of these plexuses it was distributed wholly to the former nerves. The fifth nerve as a rule belongs wholly to the sacral plexus.

For the sake of simplicity no account has been taken in these tables of the small muscular nerves derived directly from the spinal nerves, of the relative size of the nerves, or of the peripheral distribution of the main nerve trunks.

TABLE II. ORIGIN OF THE NERVES FROM LUMBAR PLEXUS.

number of plexuses indicated by the numerals. The numbers are placed under Roman numerals representing the spinal nerves which give rise to direct branches to the peripheral nerves in question. The "c" represents a branch of communication between two spinal nerves. Thus  $\frac{XI}{c} \frac{XII}{3}$  indicates that the ileo-hypogastric arose in one case from the twelfth thoracic nerve when there was a proximal branch connecting the eleventh with the twelfth thoracic nerve. The percentage at the bottom of some of the columns indicates the ratio between the number of plexuses in which the given spinal nerve is distributed to the peripheral nerve in question and the total number of plexuses examined. In making the percentages it is not assumed that a given spinal nerve sends fibers more than one segment below through the communicating branches.

There is little need of an extended review of the conditions tabulated. The nature and variety of the relations of the nerves leaving the plexus to the spinal nerves forming it is shown in the tables.

Eisler, Paterson, and others who have examined the lumbo-sacral plexus in man and other animals have pointed out that the plexus as a whole may vary considerably in relation to the spinal nerves composing it. It may present a very high form in which a given spinal nerve plays the rôle usually played by the one just below or a very low form in which the reverse is true. The plexus may vary anywhere between these two extremes. They have also mentioned that the various parts of the plexus may vary as well as the plexus as a whole. Not enough stress has been put upon this latter point however. Thus for instance one might expect, from the association of the eleventh thoracic with the plexus, the existence of a general "high" form, yet this was the case to a marked degree in none of the six plexuses into which the eleventh nerve entered. The entrance of the fifth nerve into the lumbar plexus likewise was associated with a general marked low form in but two of the eight bodies in which the condition was found.



NOTES ON THE PERIPHERAL NERVOUS SYSTEM OF *MOLGULA*  
*MANHATTENSIS*.

By G. W. HUNTER, JR.

These observations were made during the summer of 1897, at the Marine Biological Laboratory. The forms used were *Molgula manhattensis* and *Cynthia partita* (Verrill). The former was the more productive of results owing the ease with which it could be freed from its tunic. Young specimens, on account of the clearness of their tissues, could be used as whole mounts.

Two methods were used for the staining of the peripheral system. *Molgulæ* were immersed in a weak solution of methylene blue (1-1000) for  $1\frac{1}{2}$  to  $2\frac{1}{2}$  hours and left in running water a few moments before dissection. A slight exposure to the air seemed favorable to the stain. Injection of a strong solution of (B. X. Meyer) methylene blue (1 to 4%) also gave very favorable results. In the latter case the blue was injected into the ovarian vein, from whence it reached the heart and was distributed over the body. After one hour specimens thus injected frequently showed the whole peripheral system sharply defined.

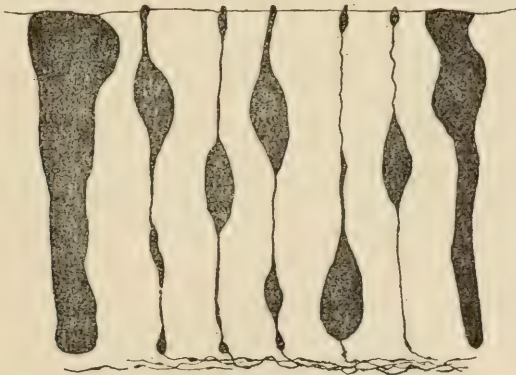
## (1). Sensory cells in the endostyle.

The endostyle in *Molgula* resembles that organ in the other Tunicates. At the bottom of the endostylar groove is found a row of flagellated cells, next come two laterally placed pads of gland cells, each pad divided by a row of deeply stained, closely packed spindle cells, the nuclei of which lie at different levels. These cells possess very short spike-like cilia and stain deeply with hæmatoxylin. Outside the glandular epithelium are found ciliated cells; the whole apparatus being bordered with a lip lined with cubical ciliated epithelium, which seems to be continuous with that of the peri-pharyngeal bands.

The sensory cells are found in the lateral position occupied by the above mentioned deeply staining spindle shaped cells. These cells are quite numerous, sometimes several hundred ap-

pearing at once under a fairly high magnification. They do not appear to be grouped in a regular manner, although they seem to be quite evenly distributed the length of the endostyle. They stop abruptly at the anterior end of the endostyle, not being found in the peri-pharyngeal bands; nor are they found in the anterior portion of the digestive tract proper.

The bipolar sensory cell as stained with methylene blue is characterized by a distal knob or spike-like enlargement, one or more enlargements situated more proximally, one of which contains the nucleus, and a more or less conspicuous enlargement at the point where the nerve fibril leaves the basement membrane. This cell, however, assumes many other forms—presumably modifications—as may be seen by glance at figure 1. The nu-



*Fig. 1.* Sensory and gland cells in the endostyle. Showing modification of the bipolar type of sensory cell. Camera drawing from several different specimens. 1·12 mm. Oc. 6 (Zeiss).

clear enlargement may be situated very near the distal end of the cell or it may, on the other hand, have a basal position and lie close to the basement membrane. In one or two cases the nuclear enlargement appeared to show fine protoplasmic branchings.

The proximal continuations of the cells after leaving the basement membrane turn sharply at right angles and run as many single loose fibrils up the endostyle. No very definite

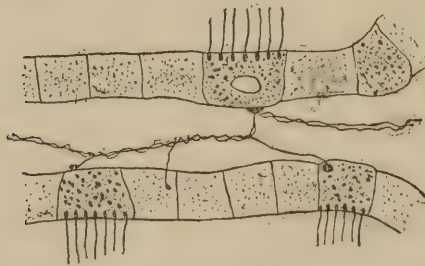
bundle of fibers is found but the fibrils seem to form a felt or basket work under the epithelium. Here and there anastomoses are found. The ultimate distribution of the fibers in the central system has not been proven. Some evidence however, points to the fibers running under the peri-pharyngeal bands and entering the ganglion by that course.

No supporting cells (*Stützellen* of authors) are found. Many gland cells are stained. They usually take the stain less intensely than the sensory cells and are large and irregular in shape.

The sensory cell in the endostyle of the Tunicates resembles the general type of sensory bipolar cell as found in Oligochaetes, Polychaetes, Crustacea, Mollusca, etc., and described by Allen, Bethe, Gilchrist, Retzius, van Gehuchten, von Lenhossék, vom Rath, etc. It, however, more closely resembles the sensory cell in the olfactory epithelium of *Myxine* (Retzius).

(2). Sensory endings in the branchial basket and peri-pharyngeal bands.

The outer lip of the endostyle, as well as the outer lip of the peri-pharyngeal bands, is covered with cubical ciliated epi-



*Fig. 2.* Ciliated cells in the branchial basket. Cells selected by the blue and show endings on the basal side. Ammonium picrate and glycerine. 1-12 imm. Oc. 6 (Zeiss).

thelium. Certain of these cells are selected by the methylene blue and stand out a vivid blue with the cilia also stained. Close investigation often shows contact endings on such cells. Contact endings of the same character appear on the basal side of

many other cells not selected by the blue and frequently cells are stained blue to which no nerve supply can be demonstrated so we cannot say anything definite with regards to such selective staining as mentioned above. The same type of ciliated cells with a like type of ending is found in the branchial basket on the borders of the stigmata. (See Fig. 2.)

The nerve fibers supplying the ciliated cells bordering the endostyle and peri-pharyngeal bands are applied rather closely beneath the epithelium, in many cases forming a true plexus of anastomosing fibers. It may be said however, that this plexus is limited to the fiber after it breaks up under the basement membrane to form the endings.

The endings appear to be disk, cup or knob like. Sometimes only one knob is found in contact with the base of a cell, sometimes several; the trefoil ending was infrequently found. Frequently the endings appear to be free. (See Fig. 3.)

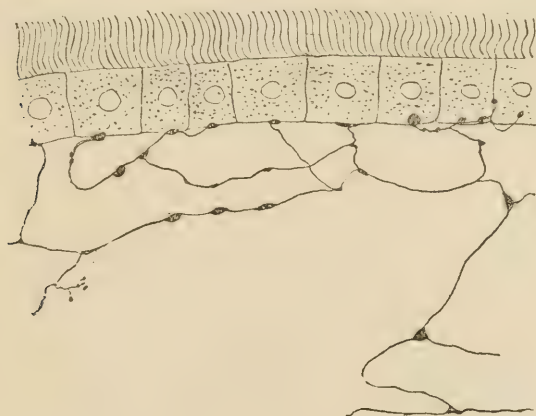


Fig. 3. Nerve endings on the ciliated epithelium of the peri-pharyngeal band. Rounded surface seen in optical section, whole mount. 1-12 imm. Oc. 6 (Zeiss).

In the branchial basket the fibers do not always remain closely associated with the basement membrane, but may follow the supporting tissue in the sinus-like interior of the branchial bars. (See Fig. 2.) Here the endings are not limited to cili-



ated cells, but are found on other cells, of a probably glandular and sensory nature. Fibrils applied closely to the basement membrane may be seen to end on the base of certain ciliated or mucous cells in disk shaped endings, then continue their course touching other cells in like manner before finally ending on a cell. (See Fig. 3.) Such endings are described and figured by Peabody in the ampullæ of Selachians and Bethe in the gustatory epithelium of the frog.

Since this work was begun I have in continuing my observations during the summer of 1898, succeeded in demonstrating:

(1). The sensory nature of the buccal tentacles and distribution of nerves to the same.

(2). The sensory nature (in part at least) of the ciliated funnel (dorsal tubercle).

(3). Sensory papillæ and sensory cells in the body epithelium.

(4). Muscle endings in the body musculature.

A later paper will contain further observations on the peripheral nervous system and its relation to the central system in *Molgula* and *Cynthia*.

Aug. 25th, 1898.

## THE ELEMENTS OF THE CENTRAL NERVOUS SYSTEM OF THE NEMERTEANS.

By THOS. H. MONTGOMERY, JR., PH.D.

(Lecturer in Zoology, University of Pennsylvania.)

The studies forming the basis of this communication were published in the "Journal of Morphology," Vol. 13, 1897.

The genera *Cerebratulus* and *Lineus* were investigated, the elements of the nervous system in the American Metanemerteans having been found, on account of their minute size, less favorable for study.

Four types of ganglion cells were found, which, in accord with the nomenclature of Bürger, may be referred to as cells

1, 2, 3 and 4. Of these the 4th type, or neurochord cells, are present only in *Cerebratulus*. All these cells are membraneless, and in all the cytoplasm has a remarkable vacuolar structure,—strands of spongioplasm bounding large hyaloplasmic vacuoles. Such a remarkably vacuolar structure does not appear to be normal in any other group of animals. In cells 3 of *Lineus* occur in the cytoplasm peculiar homogeneous, rounded bodies, which have no regular arrangement, and which are not comparable to the chromophilic granules (Nissl's granules) of other forms: for them the term *chromophilic corpuscles* was employed; genetically they seem to be local condensations of the cytoplasm. A large number of fixing reagents were employed, but after them all the axis cylinder process (I was unable to find the dendritic processes described by Bürger) presented the appearance of a single nerve tubule, and did not contain any primitive fibrils; that is to say, the outer (alveolar) spongioplasmic sheath of the cell body is continued distad to form the outer sheath of the axis cylinder, and the hyaloplasmic, structureless substance to form its core. Spongioplasmic strands may penetrate a short distance into the proximal end of the cell process, but this is an irregular phenomenon, and such strands are not prolonged to form fibrils. Thus the minute clear spaces in the fibrous core of the central nervous system represent axis cylinders, and bundles of such; and the larger and more irregular clear spaces, lymphatic tracts.

In the brain lobes and the lateral nerve chords the following connective tissue layers may be distinguished: the outer neurilemma, which is a capsule enveloping the ganglion cell layer; the inner neurilemma, a capsule separating these cells from the fibrous core ("dotted substance"). This tissue is the same as that forming the connective tissue basement membranes of all the epithelia of the body, and is formed of branching cells with a dense intercellular substance (cf. Montgomery, Spengel's "Zool. Jahrb." 10, 1897). A different tissue forms the neuroglia proper ("Hüllgewebe," Bürger). This neuroglia consists of branching cells, without any intercellular substance. Within the ganglion cell layer its elements envelope with their

branching fibers the ganglion cells, forming a loose fibrillar capsule around each of the latter; continuations of these fibers along the axis cylinder produce a sheath of Schwann. Another layer of neuroglia cells lie just on the periphery of the fibrous core, and send their branches into the latter. The only fibrils within the nervous system are those of the neuroglia and hence Bürger, who described the axis cylinder as a dense fibril, probably mistook the neuroglia fibrils for axis cylinders.

Ganglion cell 1 occurs only in the dorsal lobe of the brain; it is the smallest and probably sensory.

Ganglion cell 2 occurs on the ventral surface of the ventral brain lobe, as well as along the lateral nerve chords. These cells are arranged in radial clusters; and in the lateral chords these clusters have a regular alternating arrangement.

Ganglion cell 3 occurs on the median surface of the brain lobes, and, more sparingly, in the lateral chords. These are large, pyriform cells, and it is on them that the structure of the axis cylinder may be best determined.

Ganglion cells 4, or the neurochord cells, have been found by me only in *Cerebratulus*, but by Bürger also in *Langia*, *Prosenadenoporus* and *Drepanophorus*. (Bürger found in the two latter genera only a single pair of these cells, situated in the brain; and in *Langia* and *Cerebratulus* one pair in the brain, and a large number along the lateral nerve chords). In *Cerebratulus lacteus* I found the following distribution of these giant cells. There are 3 pairs in the ventral lobe of the brain, situated one behind the other. On the nerve chords there are none in the oesophageal region; behind the latter region they are found again, and become more numerous towards the distal end of the chords; near the proximal end of the chord they are more numerous on the dorsal surface of the chord, but distally this position is reversed. They are arranged on the chords without regularity, and there is no symmetry in the arrangement on the two surfaces of the same chord, nor on the two sides of the body. Zones where they are relatively numerous alternate with those where they are relatively scarce. About four-fifths of a worm six inches in length was serially sectioned, giving the

following figures in regard to the arrangement of these cells in the nerve chords :

<i>Right Chord</i>		<i>Left Chord</i>	
<i>Dorsal</i>	<i>Ventral</i>	<i>Dorsal</i>	<i>Ventral</i>
68	16	55	20
Total :	84		75

The axis cylinders of the neurochord cells all pass distad in the nerve chords, divide dichotomously in their course, and at certain distances show constrictions.

In regard to the "gross anatomy" the following discoveries may be noted: in *Cerebratulus lacteus* and *Lineus gesseren-sis* there is a second commissure uniting the ventral brain lobes, and in an European species of the latter genus, in addition to the second, a third. There are three commissures of the oesophageal nerves in *Cerebratulus*, and four in *Lineus*.

#### ON THE NERVE TERMINATIONS IN THE SELACHIAN CORNEA.

By CRESSWELL SHEARER,

University of McGill, Montreal.

Throughout the vertebrate body there is hardly an organ whose innervation has received so much attention as that of the cornea.

Time and again as new neurological methods have been discovered they have been applied to the study and re-study of the corneal nerve endings. Ever since 1866 when Cohenheim (1) published his celebrated paper on the termination of sensory nerves in the cornea, as demonstrated by him with his gold chloride method, down to the more recent researches of Dogiel (2 and 3) with methylen blue, an innumerable number of papers have appeared.

Despite the fact, however, that so much has been done and said on this subject, little is really known about these nerve terminations in the cornea of vertebrates lower than amphibians,



and it is surprising to find on what few types our knowledge rests, the frog, rabbit and human subject being the regular stand-bys. As nothing to my knowledge had been done on selachians I thought it might be worth while studying the conditions there presented. My results soon gave me reason to believe that this hope had not been misplaced and that the termination of the sensory nerves in the selachian cornea was evidently different from that of amphibians and mammals according to the classical researches of Hoyer, Arnold, Izquierdo, Klein, Kölliker, Dogiel, and so well worthy of further study. The following remarks apply to some short and very imperfect work which I have done on the subject within the last few months. The material I have used mostly was from the ordinary form of "Smooth dog fish" (*Mustelus canis*) so abundant here, although I have secured the corneas from the following sharks occasionally: *Galeocerdo tigrinus*, *Carcharhinus obscurus*, *Sphyrna zygaena*, *Carcharias littoralis*, for all of which the following results also hold.

The methylen blue method of staining was adopted and so far I have used it only. The particular modification of the blue method used was that recommended by Dogiel (3). Apáthy's (4) fixation also gave good results, but for thorough action Dogiel's fixation is more to be depended upon. Bethe fixation (5) has been used for sections, but on account of the trouble experienced in cutting I have had few results with it, for the cornea tissue proper so hardens in the usual processes of embedding that it is nearly impossible to cut it. At first I had trouble with my fixing fluids in that they caused too much maceration. This was stopped by adding a few drops of 1-10 per cent. solution osmic acid, which was not enough to blacken the tissues, and so render them obscure.

A few words as to the general histological structure of the cornea in Selachians.

The anterior corneal epithelium is somewhat thicker altogether than that of the cornea stroma proper, composed of large cells, having centrally placed rounded nuclei. The epithelium is on an average 12 to 18 layers of cells deep, the su-

perficial cells having the usual flattened scale-like appearance, the layer next the corneal substance proper tall cubical columnar, and the cells of the middle layers present the well known "prickle" appearance. There appears to be no membrane of Bowman or of Descemet; the posterior epithelium consists of a single layer of cells. The cornea substance proper presents the usual clear laminated appearance composed of about 12-14 sheets with corneal cells and lymph canals.



*Fig. 1.* Methylene blue preparation from the dog-fish cornea showing straight unbranching inter-epithelial fibers with dark bodies  
b, 8 mm. obj. comp. oc. 4, Zeiss, Camera.

Examining one of these corneas properly stained and fixed one is struck with the great number of nerves present, their relatively straight course from the border of the cornea inwards towards the center, and their unbranching course. It is surprising to find how long some of the fibers are, going apparently in some cases right across the whole cornea. Again one notices the very regular distances they keep from one another, always more or less parallel, looking under a low power of the microscope like a series of ruled lines. This condition is very different from what Klein describes in the frog where the nerves run very irregularly, crossing one another sometimes nearly at right angles. Some of these fibers give off lateral branches which cannot be followed for any distance

and soon become lost. These lateral branches do not anastomose with one another, as can be seen from the magnified camera drawing of Fig. 3, *b*. They suggest small fibrils coming off to form a network, but the closest examination does not show this to be the case, and I am pretty certain that a true inter-epithelial plexus is wanting in Selachians. The unbranched condition of these nerve fibrils is perhaps made more striking by comparing Fig. 2 with Fig. 1, which represents a similar preparation from the cornea of one of the osseous fishes (*Prionotus carolinus*) where the irregular joining and course of the fibers is apparent, besides in the cornea of the dog-fish the fibers are much larger and thicker. These nerves are covered with a



*Fig. 2.* Methylen blue preparation from cornea Sea Robin (*Prionotus carolinus*) Zeiss 8 mm. obj. Comp. oc. 4. , Camera.

sheath which in some places pulls away from the fiber axis proper, leaving a clear space, at the other points swelling up. This sheath however does not in any way resemble the half medullated sheath which Dogiel (*l. c.*) has described as occurring on the corresponding nerves of the human cornea. But is most probably a result of the changes caused in the nerve fibre by the staining process, and which is always characteristically obtained when the blue method is used.

Where these nerves enter the epithelium around the corneal border small fibrils are often given off which may be traced for some distance winding in and out among pigment cells which are always collected there in considerable numbers. Many of these fibrils enter into close relation with these cells, in every case they can be shown not to end on them although sometimes forming loops around them. Some of these pigment cells presented the appearances of contraction and expansion figured by Ballowitz, but no nerve endings as he describes in relation with them.

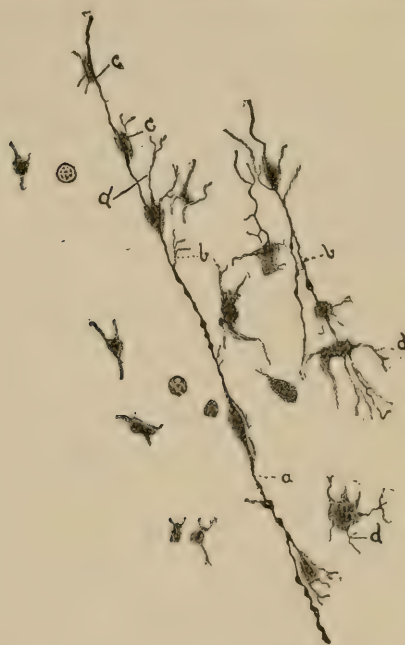
Along the course of the nerves Fig. 1, *b, b*, Fig. 3, *c*, and scattered throughout the field are seen dark staining bodies bearing processes looking like delicate nerves. These bodies will be seen to be of varying size and shape, in some places gathered together in clusters, in other places scattered and irregularly disposed. In some cases a nerve will send off a delicate fibril to one of these cells lying near to its course, in others to terminate directly in it, but generally passing on to another body further on. The processes coming off from these bodies which are shown in Fig. 3, *d, d*, wind in and out among the cells for a short distance and then become lost from view and indistinct; apparently not joining with one another. I cannot help thinking these bodies are similar to the bodies which Dogiel (2) describes as ending bodies in man. The fact that they have these processes however seems to be against this and one brings to mind the assertions of Inzani about special terminal ends situated amongst epithelial cells and which Klein (7) lays to imperfect specimens and bad technique. No bodies similar to Dogiel's complicated "knäulchen" were met with.

That these nerves and bodies are within and limited to the epithelium is easily demonstrated by transverse sections, and by macerating the epithelium off from the cornea substance proper. This method of maceration by over fixing is perhaps the best way to obtain good preparations of these nerves and bodies; in some maceration preparations the epithelium which comes off in one piece becomes broken into several pieces by the



pressure of the cover glass; these pieces will separate a little bit leaving a clear space between them. Across these spaces the nerves will be seen running from one piece to the other unbroken, showing their strength and elasticity.

Some observers have described the nerves of the epithelium as giving off short hook-like branches which bend back



*Fig. 3.* Methylen blue preparation of the inter-epithelial nerves of the Dog-fish under high magnification, showing dark bodies *c*, lateral fibers *b*; *d*, processes from the dark bodies. Zeiss homog. immers. Comp. oc. 4. Camera.

and enter into relation with stromal plexus of the cornea tissue proper and it occurred to me that these short lateral branches (Fig. 3, *b*) were of this nature; but after repeated examination I could not determine whether they did or not, but from the fact that I could not find branches running down between the deepest layer of cells towards the cornea tissue proper, I do not believe this to be the case. I have already stated I have been unable to find any true plexus or nervous network within

the epithelium which could in any way answer to the various networks described by Klein (7).

Klein states that the sub-epithelial network is situated beneath Bowman's membrane and that he was able to remove the entire epithelium without disturbing this net-work. On examining a similar preparation from the dog-fish with the epithelium so removed no trace of this plexus is found, but instead we get a view of regular plexus of the corneal tissue proper (Fig. 4) so very different in appearance from the much larger nerves of the epithelium.

This network, of which Fig. 4 is but a very poor representation, is of the very finest texture, the fibers forming it being of the very finest in size, perfectly uniform throughout their course and at once to be distinguished from the nerves of the epithelium by the way in which they branch at right angles and their irregular course and all pretty much within the same plane. Every sheet of the corneal substance proper seems to have a special network of these fibers over it. When one network is within focus the networks of the layers deeper can be faintly made out, and by properly adjusting up and down one can bring nearly all the networks into view one after the other. One peculiarity of these nerve fibers is their sharply granular appearance as if made up of a series of closely arranged dots one after the other in a delicate strand. These fibers in branching and winding about amongst the corneal cells do not keep any definite relation with them, and it is needless to say no anastomoses with them or their processes was to be distinguished. As Dogiel has found in man, the nerve fiber never comes into real relation with the cell but simply passes over it or along one border.

On comparing Fig. 4, with Fig. 7 of Dogiel's (2) paper the general resemblances of this network in selachians and man is very apparent. There is a tendency in selachians to greater regularity of branching of the fibers at right angles, they run in one direction for a certain distance then abruptly turn and run at right angles to their former course, while in man the change of direction is less sharp and sudden.

As to the distribution of this network it seems to be uniformly all over the surface of each lamella. No large trunks are ever seen to join it from the border and going to form it. The nerves composing it appear to be very continuous, where an apparent ending takes place the fiber seems to fade out in a manner which renders it impossible to tell whether it is a free ending or not.



*Fig. 4.* Fine plexus of the cornea substance proper, methylene blue, showing the right angled courses of the fibers. Zeiss homog. immers. oc. 6. Camera.

To sum up. The chief peculiarities presented by the nerves of the selachian cornea are:

1. The relatively straight, thick, nerve trunks which run in the anterior epithelium and their parallel courses with relation to one another.
2. The dark bodies into which these nerves run and sometimes terminate.
3. The unbranching condition of these nerve fibres.
4. The lack of apparent relation between the nerves of the epithelium with those of the cornea substance proper and the lack of all nerve fibers in the cornea stroma proper similar to these nerves of the epithelium.

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SOME NERVOUS CHANGES ACCOMPANYING BUDDING IN DERO  
VAGA.

By T. W. GALLOWAY.

(Abstract from Paper on Non-Sexual Reproduction in *Dero Vaga*.<sup>1</sup>)

In *Dero*, as in several other Naidiform Oligochaeta, budding is a common method of reproduction. The process, occurring wholly within a single body segment, involves the formation, from the segment, of appropriate tail parts for the anterior zoöid, and of the head structures of the posterior one. In the latter case the new formations consist of the prostomium and four cephalic segments, together with their contained structures: pharynx; ventral bristle-bundles; muscles; blood-vessels; and nervous structures, namely, the brain, ventral cord, circum-oesophageal ring, and certain small visceral ganglia, sometimes denominated "sympathetic." In the anterior individual, an anal or pavilion segment, bearing the branchial apparatus and digitiform appendages, and a preanal zone, which is concerned in the formation of new segments, are produced from the anterior portion of the bud-zone.

<sup>1</sup>Similar investigations have been made with essentially similar results, by Max v. Bock for *Chaetogaster diaphanus*.



In such a budding segment the central nervous system consists, at the beginning of the process, of the ventral nerve cord with the segmental ganglia. The cord is made up of a central fibrous mass, surrounded in the ganglionic region by cells. These cells are more numerous on the ventral surface and on the lateral horns of the cord. (Figs. 1, 2, *gn. v.*)

In the budding zone the ectoderm thickens, forming a girdle about the middle of the segment. Cell proliferations of

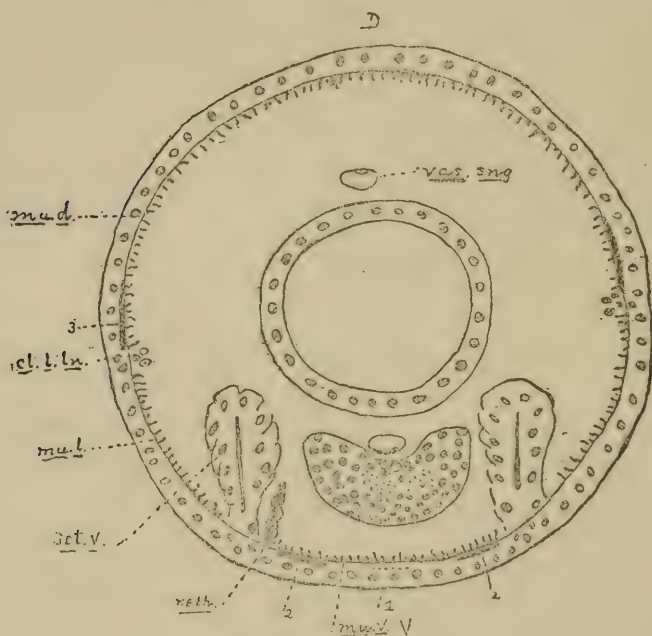
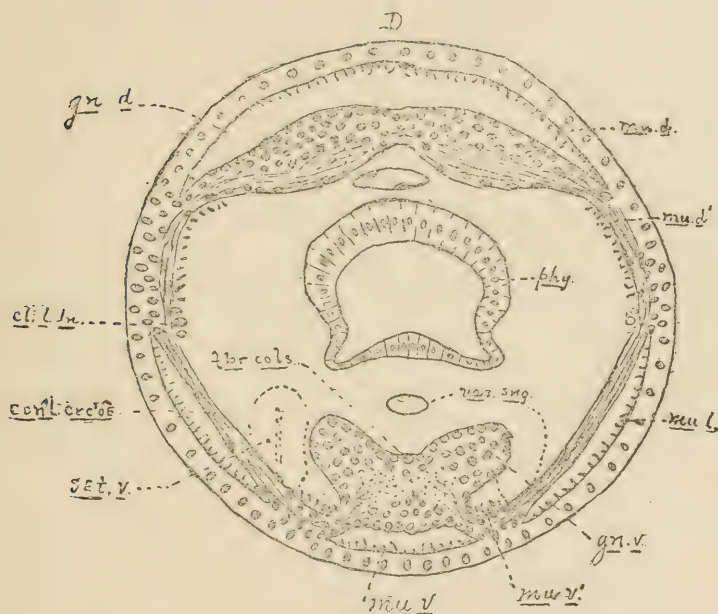


Fig. 1. (Diagrammatic). Transverse section of *Dero vaga* before budding process begins. *cl. l. ln.*, cells of the lateral line; *cont. cr. a.*, circumoesophageal commissure; *fbr. cols.*, giant fibers; *gn. d.*, brain; *gn. v.*, sub-oesophageal ganglion; *mu. d.*, dorsal longitudinal muscle band; *mu. d'*, detached portion of dorsal band; *mu. l.*, lateral muscle band; *mi. v.*, ventral muscle; *mu. v'*, detached portion of ventral band; *neph.*, nephridium; *phy.*, pharynx; *set. v.*, ventral bristle bundle; *vas. sng.*, blood vessel; 1, 2, 3, regions where the ectoderm gives rise to nervous elements.

ectoderm break through the peritoneal lining, penetrating the muscular layers, into the body cavity. If we call the band of longitudinal muscle fibers dorsal to the lateral line cells (Figs. 1

and 2, *cl. l. n.*) the *dorsal* band, those fibers from the lateral line to the ventral bristle sacs, the *lateral* bands (*mu. l.*), and the remainder, the *ventral* band (*mu. v.*), we shall be able to locate the ingrowths in a more satisfactory manner. A series of ectodermic ingrowths occurs on either side between the lateral and ventral bands. We may neglect these as they do not contribute to the formation of nervous structures, unless possibly



*Fig. 2.* Transverse section of *Dero*, showing arrangement of nervous structures in head of posterior zooid. Lettering as in *Fig. 1*.

they give rise to the small visceral ganglia lying upon the pharynx, which may be deposited as the lateral ectodermal sulci of the buccal cavity are infolded. With regard to the origin of these ganglia my evidence is as yet unsatisfactory.

The spaces between the dorsal and lateral bands are normally occupied by the cells of the lateral line, which have

usually been considered nervous.<sup>1</sup> Ectodermic ingrowths occur here, the fate of which we shall consider later. A pair of ingrowths, one on either side, penetrates the dorsal muscle band, detaching a portion (*mu. d<sup>1</sup>.*) equal perhaps to one-half the lateral band, in width. These ingrowths grow dorsally, overarch the digestive tract and bloodvessel, and unite in a median position, producing the supra-œsophageal ganglia or brain. A similar pair of ingrowths penetrates the ventral muscle band near its margin and contributes directly to the growth of the ventral cord and to the formation of the sub-œsophageal ganglia. The connective (*con't. cr'æ.*), as its fibers grow from the brain toward the ventral cord, passes superficially to the detached portion of the dorsal muscle band, re-enters the body cavity at the break between the dorsal and lateral bands,—the place of occurrence of the lateral line cells,—passes superficially to the detached portions of the ventral muscle (*mu. v<sup>1</sup>.*), and joins the ventral cord by way of the ectodermic ingrowths penetrating that band. (Fig. 2.) The circum-œsophageal connective thus comes to embrace, within its circuit, four strands of muscle fibers. These persist in this position and become functional in the posterior zoïd.

It seems further probable, from my studies, that there is a multiplication of nervous cells in the horns of the cord itself, which are responsible for at least a portion of its increased prominence.

In the preanal, segment-forming zone of the anterior zoïd, where the ventral cord is being extended caudad, there is a *median* constituent contributed by the ectoderm, in addition to the two latero-ventral contributions mentioned for the posterior individual. The cord readily shows the extent of the single median and paired lateral components, in the newer segments.

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<sup>1</sup> Since the above investigations were made Brode's excellent paper on the finer anatomy of *Dero vaga* has appeared. This author is convinced that the lateral line cells are not nervous in character. While my own investigations have caused me to hesitate in accepting the common view concerning them, I am not in a position to corroborate or controvert Brode's conclusions.

## SUMMARY.

1. The complex nervous system produced in the budding process arises either (1) from the cells of the nerve cord, or (2, and chiefly) from ectodermic ingrowths.

2. There are five regions in the ectoderm which may give rise to nervous elements: (1) a single median ventral region (1, Fig. 1) especially active in producing the median portion of the cord in the new segments of the anterior zoöid; (2) a region, on either side, superficial to the latero-dorsal muscle band (3, Fig. 1), which produces the brain in the posterior zoöid; and (3) a region on each side, superficial to the latero-ventral muscle band (2, Fig. 1), concerned in the development of the sub-pharyngeal ganglia.

3. The brain arises in the region immediately contiguous to the lateral line cells; and the ectodermic ingrowths marking the point where the connective re-enters the body cavity from its position superficial to the muscle band appear in connection with these cells. If the cells of the lateral line are nervous, they are thus brought into relation, in an interesting way, with the central nervous system. The brain, in this event, is developed in connection with the lateral line cells, while the ventral cord is derived from elements much more ventral.

## EPIDERMAL ORGANS OF PHASCOLOSOMA GOULDII.

By MARGARET L. NICKERSON.

Scattered abundantly over the introvert and body of this worm are found the epidermal organs which on the introvert have the form of papillæ, while on the trunk they are partially included in the large excavations on the inner surface of the cuticula. These bodies are ovoidal in shape with the smaller end directed outward, while the large base rests upon the circular muscle. Each is surrounded by a delicate membrane which is probably an invagination of the membrana propria.



The following is a summary of the results obtained from a study of these bodies.

1. The sensory nervous system of *Phascolosoma gouldii* is to be found entirely in the epidermal organs distributed abundantly throughout the body of the worm and the nerve fibers connecting them with the central nervous system.

2. These epidermal bodies may be grouped into four classes, two of which contain gland cells, the other two being non-glandular. The two types of glandular organs may be readily distinguished by the presence or absence of intracellular canals in the gland cells, while the two types of non-glandular organs are to be distinguished by the possession in one case of a bulb-like structure projecting above the general level of the cuticula.

3. All four classes of the epidermal organs possess sensory cells.

4. Nerve fibers are never found in continuity with the gland cells of either type of glandular organ, as has been several times asserted by different investigators.

5. The sensory cells of all these organs are bipolar, the cell body in the non-glandular organs being larger than that in the glandular organs.

6. Each of the peripheral processes of the sensory cells ends in a delicate sensory hair which in some cases at least is prolonged beyond the surface of the cuticula. In one case only, the glandular organs of the first type, the exact form of the peripheral ending was not made out.

7. The central processes of all these sensory cells enter the large nerves passing to the ventral nerve cord.

8. One type of glandular organ possesses a remarkable structure consisting of a communicating set of intracellular canals, each canal leading from an otherwise closed pouch. This pouch is surrounded by a zone of radiating threads. All these communicating canals finally open to the surface through a common duct.

9. The intracellular sacks belonging to this type of glandular organ are reservoirs for the secretion from the gland cells

and show much variation in size and appearance in correspondence with the phases of activity of these cells. The ducts from these sacks are the channels by which the secretion is conveyed to the surface of the animal. The radiating threads surrounding the sacks are probably continuations of the reticulum of the cytoplasm.

#### THE HISTOLOGICAL STRUCTURE OF THE EYES OF CUBOMEDUSÆ.

By EDWARD W. BERGER.

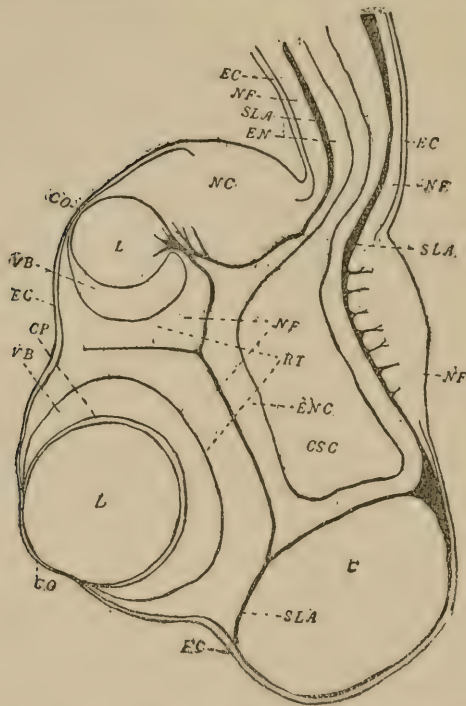
While in Jamaica with the Johns Hopkins Marine Laboratory, during the summer of 1897, Dr. Conant preserved material and tried experiments for the purpose of continuing his research on the Cubomedusæ, begun the year previous and now published as his thesis by the University. Upon the unfortunate death of Dr. Conant this material and notes were placed in the present writer's hands by Dr. Brooks. It is intended in the following paper to give only the principal results obtained by a careful study on the histology of the eyes of these medusæ, leaving their fuller discussion, together with Conant's physiological notes, for a more complete paper. The present work was done wholly on *Charybdea xaymacana*, while Conant's own work was in part done on *Tripedalia*.

For a complete description of the anatomy of the Cubomedusæ Dr. Conant's thesis, "The Cubomedusæ," or the "Johns Hopkins University Circulars," No. 132, November, 1897, should be consulted.

Roughly speaking, the Cubomedusæ, as the name implies, are cubes with their tentacles (four in *Charybdea* but twelve in *Tripedalia*) arranged at the four corners of the lower face of the cube. These tentacles are said to lie in the interradii. Half way between any two points of attachment of the pedalia (the basal portions of the tentacles) and a little above the lower margin of the bell, hang the sensory clubs, one on each side,

four in all. Each sensory club hangs in a niche of the exumbrella and is attached by a small peduncle, whose central canal is connected with one of the four stomach pockets and in the club proper forms an ampulla-like enlargement.

Each club is said to lie in a perradius, and belongs to the subumbrella, as is shown by the course of the vascular lamellæ,

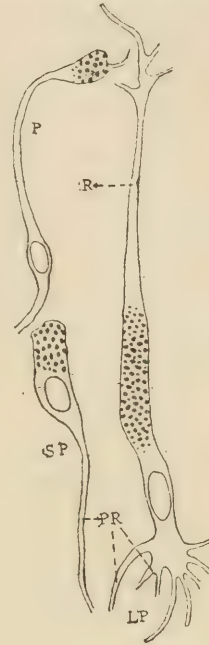


Explanation to *Fig. 1*. This is an outline taken from Schewiakoff's *Fig. 7* and is placed here to show the general relations of the different parts of a club. Since this drawing represents a section the simple eyes are not indicated. *C*—concretion cavity; *CO*—cornea; *CP*—capsule; *CSC*—cavity of sensory club; *EC*—ectoderm; *EN*—endoderm; *ENC*—endoderm of sensory club; *L*—lens; *NC*—network cells; *NF*—nerve fibers; *RT*—retina; *SLA*—supporting lamella; *VB*—vitreous body.

bands of cells, which passing through the jelly from endoderm to ectoderm all around the margin, form the line of division between sub- and exumbrella.

Each club has six eyes. Two of these on the mid-line of

the club facing inwards are called the larger and smaller (lower and upper) complex eyes because of their more complex structure, while the other four simple eyes are disposed laterally, two on each side from the line of the two complex eyes. All of these eyes look inwards through a thin transparent membrane of the subumbrella into the bell cavity. Besides the eyes and ampulla already referred to, a concretion fills the lowermost portion of the club, and a group of large cells having a network-like structure and called network cells by Dr. Conant fill the uppermost part of the club between the smaller complex eye and the attachment of the club to its peduncle. What is evidently nerve tissue, fibers and ganglion cells, fills the rest of the club. A ciliated epithelium covers the club except where interrupted by the eyes.



Explanation to *Fig. 2.* This figure represents three pigmented cells drawn from a maceration preparation of Conant's. The long pigment cell (*LP*) shows its several processes (*PR*) passing centrally, a pigmented portion, and more distally its rod (*R*) which also branches. *SP*, a short pigment cell, shows its single central process (*PR*), and distally its pigmented portion, beyond which should be continued its prism with a central fiber. This cell may also be taken to represent one of the retinal cells of the simple eyes in which case it should have a fiber at its distal end similar to cell *P* which is evidently a cell from the simple eyes.

A nerve ring, underneath the ectoderm of the subumbrella, passes from near the origin of the tentacle at the margin to the origin of the peduncle of the sensory clubs a little above the margin and gives off a branch to each club. In the course of this nerve ring are found ganglia in the interradii (pedal ganglia) and in the perradii (radial ganglia).

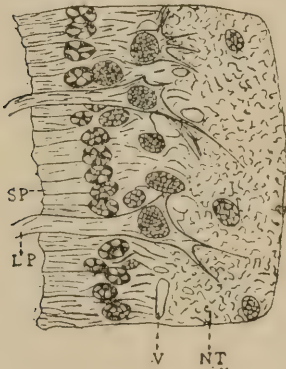
The structure of the four simple eyes may first be considered. These are little invaginated cups of epithelium, the cells of which have become pigmented. Their cells are crowded very closely in many places so that the nuclei



come to lie at different levels and many of the cells become spindle shaped. Every cell, however, extends to the cavity of the cup and ends in a rod or fiber probably homologous with the cilia of the epithelium (Fig. 2, *P*). The cup of each of eye is filled with a homogeneous substance probably a secretion of its cells and into this lens the rods from the cells project.

While Schewiakoff (Morph. Jahrb., Bd. XV, H. 1.) maintains the existence of two kinds of retinal cells (pigmented, supporting cells, and spindle shaped, or visual cells) for these eyes, as well as for the complex eyes, to be distinguished principally by their pigmentation and location of nuclei, neither Conant nor myself have been able to demonstrate any such two kinds of cells for the simple eyes.

The larger complex eye is the more complicated of the complex eyes and consists of the following parts: a cellular cornea continuous with the surface epithelium, a cellular lens, a homogeneous capsule to the lens, a vitreous body composed of prismatic elements, and a retina of pigmented cells whose central processes pass into the nerve tissue lying centrally from the retina. Figs. 1, 4, 5.

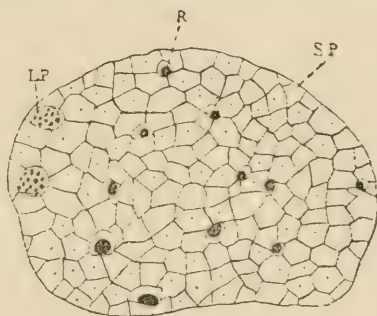


Explanation to Fig. 3. This figure shows only a small portion of a retina with its underlying nerve tissue. It shows the central processes of the long pigment cells nicely and seems to show the cells themselves in a retracted condition. This retina was killed in the dark but contained little pigment. *LP*—long pigment cell; *SP*—short pigment cell; *NT*—nerve tissue; *V*—vacuole.

pigmentation and position of nuclei as Schewiakoff maintained, but from four reasons: 1st, the pigment of the one kind, the long pigment cells (to retain Conant's nomenclature), may be

in part projected into the vitreous body while that of the other kind, the short pigment cells, is not projected; 2nd, both kinds are distally continued into rods which are readily to be distinguished by their difference in size and by the fact that the rods of the long pigment cells pass between the prisms while those of the short pigment cells pass through the prisms of the vitreous body; 3d, by a probable difference in their nuclei; 4th, by their central continuations,—the central end of the long pigment cells being continued into several processes, while that of the short pigment cells is continued into a single process. Fig. 5, also 4, 3 and 2.

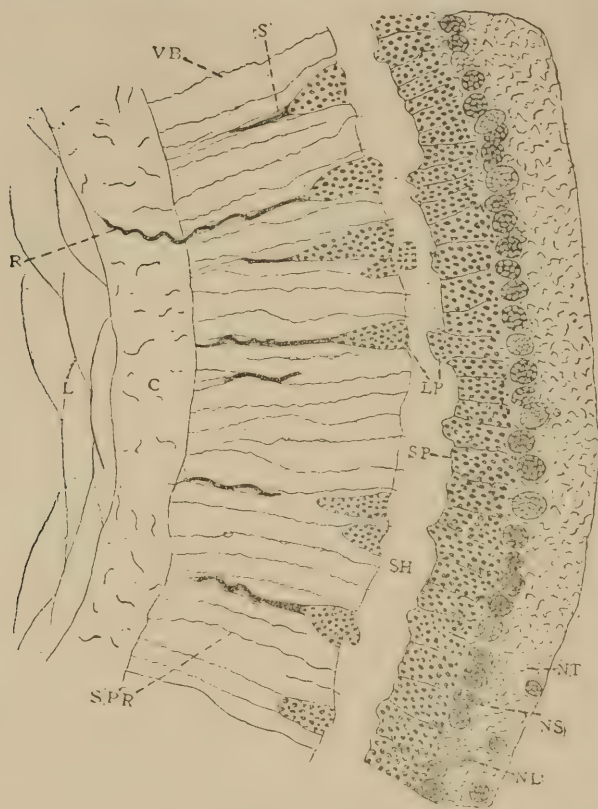
Conant maintained that two kinds of cells could not be distinguished by their pigmentation, and although he had evidence of the existence of two kinds of rods in the vitreous body he was not certain but that the short pigment cells might be changed to the long pigment cells by simply projecting their pigment. This I do not think can be the case for in the first place the two kinds of rods are too unlike and without doubt the one kind passes between the prisms while the other kind through the prisms. Conant simply left the question open, hoping to clear up the point on the new material which he preserved.



Explanation to *Fig. 4*. This shows a transverse section of the vitreous body quite near to the retinal cells. The section is not exactly transverse, but nearer to the retina on the left side than on the right, in consequence of which the pigmented portions (*LP*) of the long pigment cells are cut on the left while more to the right their rods (*R*) only are taken. These long pigment cells and their rods are readily seen to lie in the spaces between the prisms represented by the polygonal areas. *SP* refers to a prism with its central rod represented by a dot.

To Conant wholly belongs the credit of having first demonstrated the prismatic structure of the vitreous body. This can readily be seen in transverse sections of the vitreous body

where the sections of the prisms appear as polygonal areas (Fig. 4), but is not so readily demonstrated in sagittal sections.



Explanation to *Fig. 5*. This figure represents a portion of a sagittal section of a larger complex eye with a heavily pigmented retina. This retina was killed in the light and shows the long pigment cells well projected into the vitreous body. The prismatic structure of the vitreous body is not shown but the smaller lines seen in it and marked *SPR* represent the rods from the short pigment cells. Some of these rods are seen to extend into the shrinkage space *SH*. *L*—lens; *C*—capsule; *VB*—vitreous body; *LP*—long pigment cell; *SP*—short pigment cell; *R*—rod from a long pigment cell seen in this case to pass into the capsule; *NL*—nucleus of a long pigment cell; *NS*—nucleus of a short pigment cell; *NT*—nerve tissue; *SH*—shrinkage space; *S*—space about rods of long pigment cells.

As Conant suggests, each prism is evidently a continuation, a part, of a short retinal cell and not simply a secretion from

such a cell. Conant also suggests that these prisms with their central fibers are the true visual rods. What then are the long pigment cells with their rods?

Since I believe I have evidence to show that the long pigment cells can project themselves with a part of their pigment into the spaces between the prisms of the vitreous body during exposure to light while they retract themselves with their pigment when in darkness, may these cells not be solely for this purpose—to check the diffusion of light in the vitreous body?

The capsule of the lens seems to be homogeneous and according to Schewiakoff a secretion of the lens cells. The rods from the long pigment cells pass into this capsule (Fig. 5, *R.*) and the rods of the short pigment cells (better called prism cells) perhaps also do. At all events numerous smaller fibers are seen in the capsule (Fig. 5).

The lens and cornea I shall not further discuss. Schewiakoff suggests that the eye is of ectodermal origin and that it is an invagination which becomes pinched off as a hollow sphere, the outer portion of which forms the lens the inner the retina and vitreous body.

The structure of the smaller complex eye is very similar to the larger one except that it has no capsule (Fig. 1) to its lens and lacks the long pigment cells in the retina. Dr. Conant gives an excellent figure of this eye in his thesis but does not show the prismatic structure of the vitreous body nor the rods from the prism cells.

One may regard the three kinds of eyes, the simple, the smaller complex and the larger complex, as so many stages in development. The retinas, the most important parts of eyes, would be homologous and quite at the same stage of development; the lenses of the complex eyes would be homologous, but not with those of the simple eyes. The capsule of the larger complex eye stands alone. The vitreous bodies in the complex eyes being homologous cannot be homologised with anything in the simple eyes unless one regards the so-called lenses of those eyes vitreous bodies and the vitreous bodies of



the complex eyes as secretions from the retinal cells, which view does not seem probable.

Finally, it may be added that Charybdea is very sensitive to light, as is fully shown by Conant's physiological experiments, but none of these trace the seat of sensation directly to the so-called eyes of the sensory clubs, so that the evidence that these are real eyes is almost wholly histological.

Johns Hopkins University, August 23d, 1898.

#### A CONTRIBUTION TO THE NERVOUS SYSTEM OF THE EARTHWORM.

By H. R. FLING.

The past three years, under the direction of Dr. C. O. Whitman, at Chicago University, and at the Marine Biological Laboratory at Wood's Hole, Mass., I have been carrying on investigations to determine the typical segment of the Earthworm and to homologize as far as possible the head segments with the typical segment. I take this opportunity of presenting some of the reconstructions which I have made, reserving until a later time the details and discussion of homologies.

In 1894 Dr. Richard Hesse published an article entitled "Zur Vergleichenden Anatomie der Oligochaeten," in the "*Zeitschrift für wissenschaftliche Zoologie*," 3 Heft, Band 58. Besides giving a description of the nerves in a typical segment, he reconstructed the nervous system of the head segments. The following year Miss Langdon published an article "Lumbricus Agricola Hoffm," in *Journal of Morphology*, XI, pp. 193-234.

In both of these papers the arrangement of the nerves in the typical segment was described as consisting of a ventral cord with a ganglionic enlargement at the posterior part, from which two nerves take their origin, and a third nerve leaving the anterior smaller part of the cord. These three nerves, after leav-

ing the ventral cord, pass in a lateral and ventral direction through the longitudinal muscle, and each nerve divides into two branches or rami, one passing ventrally and the other dorsally between the layers of longitudinal and circular muscles. From these rami smaller nerves are given off to the basement membrane and finally these fibers reach sense organs at the surface.

Miss Langdon concluded that the dorsal and ventral rami of these three nerves were not continuous over the mid-dorsal and mid-ventral line. Dr. Hesse was not sure, but was rather inclined to think that they did not cross the mid-dorsal and mid-ventral line.

The gold chloride method has been the most helpful to me in my reconstruction. I have been able by this method to make out the following points which I shall publish later in detail with my plates.

The two nerves mentioned above which leave the ganglion in each segment, anastomose shortly after leaving it, and from the posterior of the two nerves, at the place of anastomosis, a nerve is given off to the dissepiment and walls of the intestine. The nerve has been called the "sympathetic."

The anterior of the two nerves passing from the ganglion or the middle nerve of the segment sends its dorsal ramus close behind the ventral and dorsal pair of setæ and fine branches are given off to each pair of setæ.

In all the forms I have examined I find that the dorsal and ventral rami of the anterior and posterior nerve of each segment are continuous over the mid-dorsal and mid-ventral line and that the dorsal and ventral rami of the middle nerve of each segment as they approach the mid-dorsal and mid-ventral lines break up into finer branches and anastomose with the anterior and posterior nerves of the segment, making a very fine network.

From specimens which had been cut near the mid-dorsal line and flattened out, I have sections showing anastomoses of these dorsal rami from the dorsal setæ to the dorsal pore and from the ventral to dorsal setæ.

In *Allolobophora foetida* the posterior nerve from the gan-

gion gives off from its dorsal ramus another nerve which runs parallel to the posterior dissepiment and gives off branches to it.

According to my reconstructions the fourth segment is a typical one. In the third segment the middle and posterior nerve leave the cord as a single nerve but soon divide into the typical middle and posterior nerves. In the second segment the same thing is found as in the third segment, although the middle and posterior nerves travel a much longer distance as a single nerve, before they break up into the typical nerves in the second segment. In the first segment, two of the nerves take their origin from the sub-oesophageal ganglion, and one from the commissure; these nerves passing into the first segment form an anastomosis between the circular and longitudinal muscles very similar to the condition found in the other segments.

The prostomium is innervated by a large double nerve from each side of the brain. These nerves divide into numerous branches as they approach the anterior end of the prostomium.

From either side of the commissure two nerves are given off which form a network around the oesophagus and pharynx. This is very similar to the arrangement which Dr. Bristol found in *Nephelis*.

A COMPARATIVE STUDY OF THE FUNCTIONS OF THE CENTRAL  
NERVOUS SYSTEM OF ARTHROPODS. A BRIEF SUMMARY  
OF THE RESULTS, BY ALBRECHT BETHE.<sup>1</sup>

Translated from the German

By W. W. NORMAN.

The brain (supraoesophageal ganglion) of the Arthropods is to be regarded first as an inhibitory organ; in addition to this it exercises a tone upon the musculature of the whole body. It is also of course a central organ for the parts of the body innervated by it. It is not however the seat of co-

<sup>1</sup> *Pflüger's Archiv*, Bd. 68, p. 449.

ordination of motions (Burmeister, Lemoine and others), of direction (Fauvre), or of a general center of motions (Steiner). The animals experimented upon by me include the most distantly related forms,—species in which in reference to segmentation, and body-proportions the greatest differences prevail. In all of these forms section of the oesophageal commissures (or removal of the brain, in which naturally the organs innervated by the brain no longer came into consideration) was in no case followed by paralysis in a single movable organ. Likewise all of the more complicated reflex actions, which can be observed in the normal animal (with the exception of such as are to be regarded as having connection with both brain and ventral cord) remain after isolation of the brain, as compensatory movements of the eyes, walking and swimming movements, flying movements, turning over when placed on the back, eating, copulation, cleaning legs and body, etc. [With *Carcinus* the possibility of forward motion is lost. This is, however, a special case, which will be more fully explained in a later paper]. All motions are changed in so far as the tone of the muscles is changed from that existing in the normal animals. I am of the opinion that to this alone are due all the irregularities which appear in walking, swimming and flying. The essential point, it seems to me, is that all the reflexes are still possible (auslösbar).

The changed tone which appears on removal of the brain, is due to a general lowering of the muscular force, which may be readily observed (especially if one of the commissures be cut), in the case of *Carcinus*, *Astacus*, *Squilla*, and *Dytiscus* by the difference in pressure exerted by the muscles of the two sides against the hand of the observer. (In the case of *Carcinus* this difference was actually measured.) The changed tone may also be observed in the stronger tension of certain muscle groups over others, chiefly the flexors over the extensors. This is shown by the position of the extremities, which after the operation remain more strongly flexed than normally, especially in the coxal joints, thus causing the body to be held higher than usual and in case of section of *one* of the oesophageal commissures, or of removal of one half of the brain the



body is turned to one side (*Carcinus*, *Astacus*, *Pachytylus*, *Apis*, *Dytiscus*). The lowering of the muscular tone is, however, perhaps plainest to be seen in the case of those animals, in which the body-segments are movable against each other. Here is always to be seen a curvature of the body toward the uninjured side, when the operation is made on one side only (*Astacus*, *Squilla*, *Apis*). From this and from the fact that only the extremities of the operated side of the body are held abnormally after section of an oesophageal commissure, it follows that each half of the brain exercises a tone only or chiefly upon the same side of the body.

The above conclusion is hinted at from the changes of tone in the organs which are innervated by the brain. For example there is observed a change in the position of the eyes of *Carcinus*, *Astacus*, and *Squilla*; of the first pair of antennæ in *Carcinus*, of the second pair of antennæ in *Astacus* and *Squilla* and the antennæ in *Hydrophilus*. This change in tone is particularly well shown through the asymmetry which arises after section of one of the oesophageal commissures and extends here chiefly to the organs innervated by that half of the brain situated on the same side. Is it to be concluded from this, that the ventral cord exercises a tone upon the parts of the body situated in front in the same way as the brain does on the parts of the body situated more posteriorly? At most, only the suboesophageal ganglia could be considered since after section of the commissures behind this ganglionic mass a change in the tone of the organs of the head no longer takes place, and, further, changes of the front part of the animal (in front of the section of the ventral cord) after cross-section of the ventral cord can under no conditions be confirmed.

It has been claimed that Arthropods after removal of the brain cease to make spontaneous movements. If we are to understand by spontaneous motions that an external stimulus is not evident for the origin of the motion or for the change of one form of motion to another, then spontaneity is present in all of the Arthropods observed by me after removal of the brain. It was best demonstrated in the case of *Astacus*, where

the animal resting quietly suddenly begins the walking-movements without changing position, then stops these and begins to rub itself, etc.

The assertion that the brain of Arthropods is an inhibitory organ is supported by the following facts :

1. It was observed in almost all of the animals experimented upon, that reflex actions of an animal deprived of its brain are called forth by such stimuli as under normal conditions fail to cause a reaction.

2. The animals operated upon are in almost continual motion and rarely make a pause, while the same animals under normal conditions often remain quiet for a long time and execute movements only when there is cause. *Astacus* and *Carcinus* work the mouth organs almost unceasingly even when they have no food ; also even without the application of any stimulus. *Carcini*, *Astaci*, *Squillæ*, *Apes* and *Dystici* deprived of their brain, rub themselves by the hour, or make, even when lying on their backs, powerless walking movements. The only animal in which this was not clearly the case was the grasshopper (*Pachytylus*). Through lack of inhibitory impulses the motions of the animals are purposeless. The inhibition arising from each half of the brain extends only to the corresponding side of the body, since only upon that side of the body on which the oesophageal commissure is cut, or the half of the brain is removed appear the continued actions of the extremities. This increase in motion upon the operated side is very plainly present in all of the animals upon which I operated, indeed even in *Pachytylus* it is decidedly expressed, where extirpation of the whole brain gave no definite result. The strongest proof for the inhibition theory is the circular motion to the side of the uninjured half of the brain, which appears *always* in the case of some animals (*Pachytylus*, *Apus*), frequently in the case of others (*Astacus*, *Squilla*, *Dytiscus*), after removal of one half of the brain, and which I believe must be referred solely to the freedom from inhibition on the operated side of the body.

It is not a forced movement as Fauvre and Steiner suppose; does not depend upon a center of direction (Fauvre) situated in the brain; nor is it a general center of motion (Steiner), since after removal of the inhibition of the uninjured side through applied stimuli forward motion and even *circus* motion to the injured side may be called forth in any of the animals experimented upon except the *Brachyura* (*Carcinus*), in which here the *circus* motion to the right or left (toward the uninjured side) is a forced one. This rests on the fact that upon the operated side the lateral motion becomes impossible, and forward motion appears in its stead, while the legs of the uninjured side continue to go sideways.

3. In the case of animals with negative phototropism it was established that this property is lost after longitudinal splitting of the brain (*Carcinus*, *Astacus*, *Hydrophilus*). As for *Carcinus* the same effect could be produced by removal of the globuli.

4. The mouth ganglia (suboesophageal ganglion) are in no arthropods (that I have investigated) the seat of all co-ordination of motion. In the case of *Astacus* and *Carcinus* they play the greatest rôle; here progressive motion, the possibility of holding the body on its legs, or of turning over when placed on its back are all lost. Paralysis, however, is not caused in a single segment of the posterior animal, and other complicated reflex actions as the motions of eating, of cleaning body and legs, etc., are still retained (*Astacus*, *Carcinus*). The effect of the removal of the mouth ganglia is not so marked in *Squilla*, *Pachytylus*, *Apis* and *Hydrophilus*. Progressive motion is still possible for *Squilla*, and in addition that of turning from the dorsal to the ventral position for the other three; the wing movements for flying in the case of the grasshopper and the bee; the reflex actions of swimming in the case of *Hydrophilus*, and of jumping in the case of *Pachytylus*; that is to say, all that the posterior animal is able to do is retained,—only there is in general a certain awkwardness and feebleness in the mentioned activities.

5. The degree of independence of the individual thor

acic ganglia, appears to vary for different animals. Only *Astacus* and *Hydrophilus* were more accurately studied as to this point. For *Hydrophilus* the three thoracic ganglia are equally coordinated centers, each being the center for the various reflex actions of the corresponding segment. On the other hand, in the case of *Astacus*, when the ventral cord is cut through between the first and second pair of walking legs there is a greater loss than when the section is made just behind the mouth ganglia; there is not only the loss of progressive motion, but also the movements of feeding. All other movements, particularly those of flexion and extension are localized in the ganglia of their respective segments.

6. Section of the transverse commissures between the halves of one or more ganglia produces no paralytic effects; for example, longitudinal section of the brain of *Carcinus*, *Astacus*, *Apis*, *Dytiscus*; similar sections of the thoracic ganglia of *Astacus* and *Carcinus*. It follows from this, that the motor elements for each half of the body lie in the corresponding halves of the ganglia, or at least that all the motor impulses to a muscle in no case make a total crossing in the ganglia.

7. The influence which the brain or any part of the central nervous system exercises upon the parts lying more posteriorly is conducted along one side only of the ventral cord, i. e., no crossing through the transverse commissures. (If a longitudinal commissure is cut through, the symptoms appear only along one side of the animal—*Astacus*, *Hydrophilus*).

8. A stimulus from the brain along the ventral cord is conducted with a local signal, i. e., so that a locally (or definitely) directed reaction follows, *only* through the oesophageal commissure of the stimulated side.

9. The transverse commissures of the brain can conduct impulses to the longitudinal commissure of the other side and thus to the ventral cord, but not in such a way as to bring about a definite reflex action; and even then the stimulus must be very strong.

10. It may be concluded from the experiments on the crayfish (*Astacus*), which have been in part confirmed upon



Carcinus and Hydrophilus that (a) an impulse can be conducted along the entire length of the ventral cord along one side only, i. e., through the longitudinal commissure of the side receiving the stimulus in such manner as to call forth a locally (definitely) directed reflex action. (b) The transverse commissures of each ganglion are the only paths along which an impulse calling forth a locally directed reflex action can be transmitted from the stimulated side to the other one.

#### THE FUNCTIONS OF THE OTOCYST. A REVIEW.

By E. P. LYON.

Up to the year 1887 it was generally believed that the otocyst as found in invertebrates was an organ of hearing. The resemblance of the capsule, with its sensitive hairs and otolith, to the ear of vertebrates was the main ground for this belief. Indeed "the otocyst was regarded as a reduction or rudimentary state of the membranous labyrinth." After the development of a definite theory of equilibrium and geotropic functions for the vertebrate ear, it was natural to expect that similar functions were subserved by the invertebrate otocyst. Some of the work which has been done in support of this view I shall briefly review.

I. The first paper, that of Delage, *Sur une Fonction nouvelle des Otocystes*, appeared in the *Archives de Zoologie Expérimentale et Générale* in 1887.

After trying mollusks of various kinds with little success, he turned his attention to crustaceans. A description of the behavior of two species will be sufficient to serve as a general index of Delage's work. The schizopod *Mysis* has its otocysts in the inner plates of the four-parted tail. The cysts could therefore be removed with ease. On account of their distance from the more delicate parts of the central nervous system the operation would seem likely to be free from severe shocks and

from permanent after-effects due not to the removal of the organs but to injury to remaining parts.

If only the otocysts were removed from these animals, they swam normally and no peculiarities were observed in their behavior. But when in addition the eyes were removed, the animals were "completely disoriented." Even many days after the operation, when the wounds had entirely healed and the animals had recovered their normal activity and appetite, "correct and normal swimming remained impossible." But it is important to observe that forced movements were present. For hours, even days at a time, the operated animals would roll around a longitudinal axis in one constant direction or turn somersaults. Such appearances would seem to indicate something besides a loss of equilibrium. In spite of the apparent excellency of this animal for such experiments, it is probable that some one-side injury to the nervous system resulted from the operations.

The extirpation of neither eyes nor otocysts alone was sufficient to cause disturbance of equilibrium. But loss of the eyes and mutilation equivalent to taking away the otocyst-containing lamellæ of the tail but without molesting these (for instance, cutting away the outer tail-pieces) caused no equilibrium disturbances. Therefore Delage infers that the inner lamellæ with their otocysts are not a mere mechanical factor to equilibrium but that the otocysts constitute a true geotropic organ regulating the orientation of the animals with reference to the direction of gravity.

Experiments on the decapod *Palæmon* gave somewhat similar results. Loss of the antennules with the contained otocysts caused no difficulties of locomotion. Hardly any troubles followed loss of both otocysts and eyes. But when in addition the filaments of the antennæ were cut away, the animals were manifestly and permanently disoriented. It is likewise imaginable that if a man had both legs, both arms and both eyes removed, he would have some trouble getting about in the world. However, as animals equally mutilated but without disturbing the otocysts were not troubled in the same degree and manner,

Delage believes that his experiment proves the equilibrium function of the otocyst.

He believes that the otocyst affects locomotion reflexly and not by arousing sensations followed by voluntary acts. He inclines, however, to the belief that this reflex control of locomotion is accompanied, or rather followed, by true sensations of movement. "These sensations as well as the preceding reflex acts may be aroused by the mechanical action exercised during movements by the liquid or by the otoliths upon the nerve terminations in the walls." The otocyst, according to Delage, is a double organ mediating sensations both of sound and of movement. According to his experiments sight and touch can compensate largely for loss of the otocysts so far as locomotion is concerned.

II. *Gleichgewicht und Otolithenorgan* by Max Verworn, Pflüger's *Archiv*, V. 50, P. 423.

After the appearance of Delage's paper Engelmann gave public expression through the *Zoologische Anzeiger*, 1887, of a view which he had privately entertained for several years. He held that the otolith of the Ctenophors is "an apparatus for the regulation of the equilibrium of the body." Verworn undertook to prove Engelmann's conjecture experimentally. Of the Ctenophors studied *Beroë ovata* gave the best results. This species more regularly than any other assumed definite equilibrium positions. The animals come to rest with the body axis in the vertical, either at the surface of the water with oral pole directed upward or on the bottom with oral pole downward. They are able, Verworn asserts, to change their specific gravity and therefore the same individual is found at one time at the surface in the first position, at another time on the bottom in the second position. . If *Beroë*, standing at the surface with its mouth directed upward, was carefully turned by means of a glass rod into some other, say the horizontal, position, the swimming plates of the under side immediately began making vigorous strokes toward the aboral pole, while those of the upper side remained quiet. As a result, the animal turned back toward the vertical resting position. Just before it reached the

vertical, the plates hitherto inactive would begin vibrating, so that any swinging beyond the vertical was prevented. For any change from either equilibrium position the general result was the same, namely a definite and orderly series of movements bringing the animal back to its normal resting position.

The otolithic apparatus in the Ctenophors is situated at the aboral pole at the junction of the eight meridional ciliated grooves which run from the otolith toward the oral pole and broaden out into the swimming plates. These plates, indeed, are composed of cilia joined together. The otolith could be seen easily through the transparent apical tissues. In some species it could be removed by thrusting a glass tube through the unresisting substance and sucking away the stone. In *Beroë* it was necessary to burn out the stone with a hot needle. After the operation, although the animals recovered from the shock and atelike normal individuals, they never again assumed definite equilibrium positions. It was noticeable, however, that the different rows of swimming plates of the operated animals were entirely independent of each other. Each now maintained its own rhythm. Some rows would be motionless for considerable periods, while others were in active vibration. This Verworn thought due to the destruction of the regulating apparatus. But Romanes and others have shown that any break in the tissue connection of the ciliated furrows leads to independent rhythm in the different rows of plates, under which condition it is not to be expected that any definite resting position would be assumed. The validity of Verworn's conclusions has been doubted on this ground. It has been asserted that he destroyed the unity and therefore the coordination of the locomotor system and even though the animal might have twenty geotropic organs, it could no longer assume its characteristic orientation.

In anticipation of this criticism, Verworn introduced a sharp needle through the mouth of several Ctenophors and attempted to destroy the tissue lying under the otolith without disturbing the latter. After a few minutes the animals assumed the equilibrium position. Such experiments are however of doubtful value and the criticism of Verworn's work retains



much force. In one case equilibrium lost by destruction of the otolith was regained, after two days, by means of (or at least coincident with) the regeneration of the stone. More observations of this kind would have strengthened his position greatly.

As to the mechanism by which the equilibrium position is assumed, "It is easily intelligible" says Verworn, "that the varying pull and pressure which the otolith exerts upon the hairs between whose ends it is suspended, must call forth a varying stimulation in the hairs, which expresses itself in a stronger or weaker activity of the cilia or in a total cessation of the same." Being unable to prove any response to sound on the part of Ctenophors, Verworn believes the otolith to be solely a geotropic organ and proposes the names "statolith" and "statocyst," in place of otolith and otocyst, as terms which recognize what he considers the true function of the organs.

III. *Weitere Beiträge zur Physiologie der Ohrlabyrinthes*, A. Kreidl, 1893, *Sitzungsberichte der K. Akad. d. Wiss., Wien.*, V. 102, P. 149.

Kreidl worked upon *Palæmon*, the same crustacean that Delage had used. At each moulting these animals, like the crayfish and many other crustaceans, cast off the otoliths together with inner lining of the otocyst. Afterwards, by means of their chelæ, they place fine grains of sand or other hard particles within the cyst to act as otoliths. Kreidl placed *Palæmon* immediately after moulting upon finely powdered iron, and the animals placed this in their otocysts. If an electro-magnet was brought near, the iron otoliths were attracted and the animal responded to the magnet in the same manner as to the force of gravity. Suppose the magnet were placed at the animal's right side, the crustacean "would have the sensation" of being inclined to the right and would turn so that its sagittal plane lay in the line of the resultant of the forces of gravity and the magnet, just as this plane was in the vertical when gravity was the only active force. This experiment of Kreidl's is perhaps the most satisfactory as well as the most ingenious that has been performed. It surely seems that the orientation of the animals with respect to gravitation is effected through

the otocyst. But the assumption that a sense of equilibrium exists in invertebrates—the assumption that they feel the direction of the vertical—seems unjustifiable. Indeed, when we consider how perfectly in ourselves equilibrium is maintained by purely reflex processes and how rarely we “feel” our position in space, in the sense that we taste or smell or hear or recognize any external phenomenon whatsoever by means of a sense organ, it seems extremely improbable that these low organisms have a recognition of the vertical. As Cyon facetiously remarks it presupposes too high a degree of mathematical learning on the part of these low forms.

Kreidl also tried removal of the otocysts from *Palæmon* but, instead of cutting away the eyes as did Delage, he covered them with black paint. The same lack of orientation followed this treatment as did the more severe operation of Delage, and of course every experiment which avoids removal of parts is more satisfactory and convincing.

IV. *The Otocyst and Equilibrium.* Clark, 1896, *The Journal of Physiology*, V. 19, P. 327.

The chief interest in this paper lies in the author's claim that the otocyst without the otolith is able to function as an equilibrium organ. Clark worked upon the decapod crustaceans, *Gelasimus* and *Plathyonichus*, both of which have no otoliths in the cyst but are very active and would seem to need an equilibrium organ. He studied carefully the compensatory motions of the eyes accompanying passive rotation and bases his conclusion largely on these. As is well known, when a vertebrate (or a crustacean also, as Kreidl found), is rotated slowly the animal's eyes turn in the opposite direction, or in other words, tend to retain their positions in space. If the rotation of the animal is such as to change its orientation with respect to the vertical, the compensating eye positions are retained until the original position of the body is restored. These motions therefore seem closely connected with equilibrium. After removal of the otocysts, Clark found that the geotropic compensating motions of the eyes were lessened. When in addition the eyes were blackened, the motions failed altogether; or at

any rate none could be detected with the means of observation and measurement employed by him. The animal now seemed to have no appreciation of the vertical or recognition of its position relative thereto. In locomotion likewise the animals were uncertain and timid after these operations. As a result of all his experiments Clark believes that the otocyst without the otolith is able to act as an equilibrium organ.

Although Bethe has argued that the stone is a necessary part of an equilibrium organ, Clark's view would seem at least as defensible in theory as it is demonstrable in fact. Even though no stone or body of great density be present, it is true that with every change of orientation with respect to the vertical, new stress relations between the parts of an organ must be set up. These would be especially strong in hairs projecting into a cavity. In one position of the body it might be that the weight of a hair would press perpendicularly upon its base. In another position of the body, the same hair would pull upon its base. Or it might be bent to one side. It is true that this pull or bend would be small, especially is a cyst filled with liquid. But we know that a very small stimulus is sufficient in these organs to call forth a response. Nor do we need to imagine a movement of the hair as a whole. A mere change in the stress of its cells or of parts of the cells might act as a stimulus. Such a supposition indeed would go far toward harmonizing the diverse phenomena of geotropism. Many infusorians have a definite orientation in the water. It is known furthermore in many cases that different parts of the cells, for instance cytoplasm and nucleus, have different densities. It is imaginable that the pull of the nucleus in one direction or its pressure in the other might render the ciliary action on one side different from that on the other; that only in one orientation, (for instance in *Paramoecium*, with anterior end directed upward) would the action of the cilia on opposite sides of the body be equal. In plants too, geotropic phenomena must be traced back to the cells. I have mentioned the nucleus and cytoplasm only as parts whose stress relations may possibly be changed by gravity. The large and complex molecules of living matter

constitute another possibility of geotropic orientation. Surely it seems that, while otolith and otocyst are probably devices for strengthening and rendering more definite the geotropic response, yet it may turn out in the end that protoplasm itself possesses geotropic irritability.

AN EXPERIMENT TO TEST RECENT THEORIES AS TO MOVEMENTS  
OF NERVE CELLS.

By HENRY H. GODDARD,  
Clark University, Worcester, Mass.

The following experiments of Mr. Goddard were reported by Dr. Hodge :

Considerable attention has been directed in recent years toward attempting to explain various functional states of the nervous system, hysterias, sleeping and waking, even psychic conditions, association of ideas, memory and forgetting, by amoeboid movements of nerve elements. For the most part, when announced, these theories have had about as much foundation in experimental evidence as similar ancient theories as to flow of "spiritus animalis" or ideas of making and breaking of electric contacts between nerve fibers and nerve cells, before the fibers were discovered to be outgrowths of the cells.

In line with Ramón y Cajal's theory, that the dendrites represent receiving poles, attention has tended to focus on these processes, especially on their terminal twigs and more especially still on their gemmular expansions, the "contact granules." Berkley, in 1895, in chronic alcohol poisoning, and in 1896, with a number of other pathological conditions, pointed out the fact that the terminal twigs of the dendrites, as well as their proximal portions in some cases, presented, instead of their usual appearance, a beaded, moniliform, varicose condition, with very few contact granules or none at all. He naturally attributed these appearances to the pathological causes in question, although, before doing so, it would have been safer logic to have studied first the possible changes dependent upon phases of normal function. About the same time Demoor (La



Plasticite Morphologique des Neurones Cerebraux, 1896), obtained precisely similar findings in animals poisoned with morphine, chloral hydrate, chloroform and also in those whose cerebral cortex had been stimulated electrically (for only five minutes). He also investigated, in no very adequate manner, normal conditions of rest and fatigue, but with wholly negative result.

The following experiment was devised to obtain preparations of nerve cells quickly enough, if possible, to catch them in their sleeping and waking states. It consisted simply in cutting through the entire head of the animal at a single blow with a very sharp thin knife, the parts of the head falling instantly into large culture dishes of Cox's solution, warmed to 39° C. In the two experiments to be described puppies, about seven weeks old, were used, sisters from the same litter. It was hoped by using the surfaces coming first in contact with the killing fluid, to obtain the cells before they could extend or retract, in case their processes actually changed position.

In the first experiment one puppy was killed at 4 o'clock P. M., awake, though rather sleepy, after having played about actively the greater part of the day. The sister puppy was kept awake from this time until 7 P. M. of the same day, when she was allowed to go to sleep. Thinking that sleep might reach its maximum depth in about 1½ hours, it was intended to cut the brain at 8:30. However, after sleeping soundly until 8:05 she suddenly opened her eyes, yawned, stretched and got up, evidently pretty well awake. By very gently laying her in position again, however, she was asleep by about 8:10 and the cut was made, after being asleep again for only 5 minutes, at 8:15. Results of the experiment may be seen in the following table, as related to the pyramidal cells of the cerebral cortex.

	Puppy awake, 4 P. M.	Puppy asleep, 8:15 P. M.
Cells with dendrites not varicose,	211	107
Cells with dendrites slightly varicose,	36	3
Cells with considerable varicosity of dendrites,	12	6
Cells with much varicosity,	49	1
Whole number studied,	308	117
Cells showing varicosity,	31.1%	8.5%
Cells with much varicosity,	15.9%	0.8%

The appearance of the specimens was even more striking than might seem to be indicated by the table, but, as far as the mere state of waking and sleeping is concerned, the result is the reverse of that called for by current theories. In the sleeping animal, where contacts should be interrupted, the contact granules being retracted into the moniliform swellings, the dendrites are, almost all of them, beautifully expanded. In the waking animal, where perfect contact of the cells is called for, a large percentage are retracted and varicose. The result, if it can be taken to indicate anything, clearly tends to confirm Demoor's experiments, extending his results, moreover, into the sphere of normal functional activity of the cells. According to this view the varicosity of the dendrites corresponds to a fatigued or abnormal condition, whether awake or asleep. The waking puppy, in our experiment, was partially fatigued; the sleeping puppy, partially rested, the 1 hour and 10 minutes sleep having sufficed, however, to bring the cells into a pretty completely rested condition in this respect.

The second experiment was made with the purpose of definitely testing this point. The first of two sisters was taken on waking in the morning, at 7 o'clock. The second was kept awake, playing and running about the entire day, until 5:40 P. M., when it became practically impossible to keep her awake without doing violence to normal conditions. After five minutes sleep, the cut was made at 5:45 P. M.

It is difficult to find a single varicosity on the dendrites of the morning puppy. For long distances in the cortex of the evening puppy it is difficult to find a cell whose processes are not more or less varicose. The results are certainly as striking as those obtained by either Demoor or Berkley for pathological conditions. The experiments are being continued by Mr. Goddard, but confirming and extending Demoor's work, as they do, it was thought advisable to make the above brief report.

Specimens showing the above points were demonstrated.

## ANNOUNCEMENT.

It gives us great pleasure to announce the addition of three collaborators to the editorial staff of the JOURNAL since the appearance of our last issue. These and the departments of which they will have oversight are as follows.

C. F. HODGE, PH.D., *Professor of Physiology and Neurology, Clark University*; Neuro-cytology, especially functional changes in nerve cells.

G. H. PARKER, S.D., *Instructor in Zoology, Harvard University*; The sense organs and nervous system of the invertebrates.

A. D. MORRILL, M.S., *Professor of Biology, Hamilton College*; The sense organs of the vertebrates.

Contributions for publication and books and reprints for review pertaining to these departments may be sent either directly to the collaborator in the proper department or through the publication office of the JOURNAL.

The concluding number of Vol. VIII will contain the remainder of Dr. Meyer's Review of the Data of Modern Neurology, and a contribution upon the "Growth of the Brain of the Frog" by Dr. Donaldson, together with other articles.

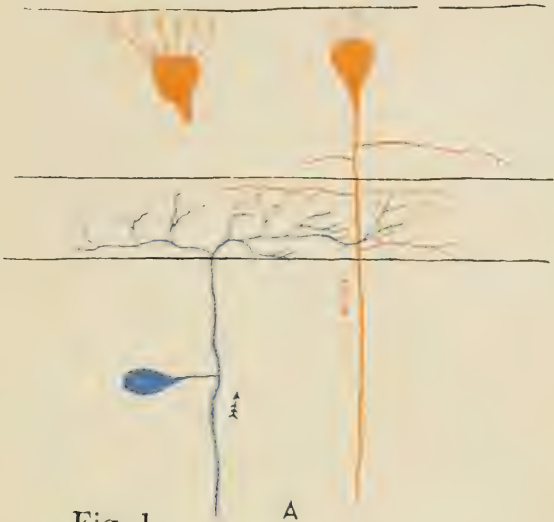
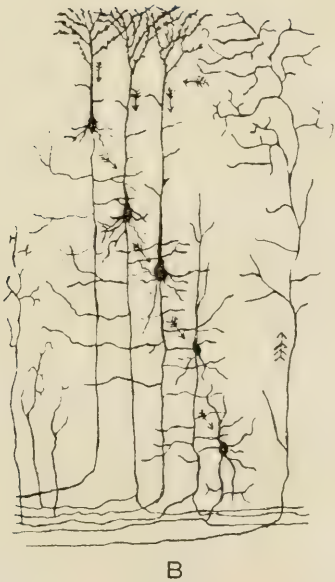


Fig. 1.







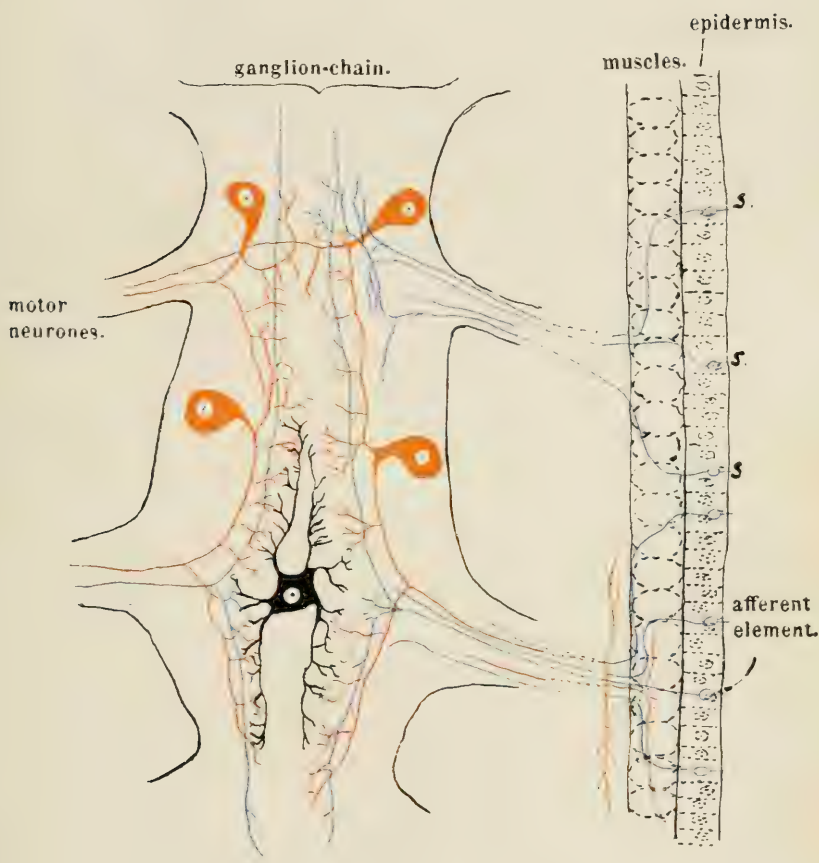


Fig. 2.



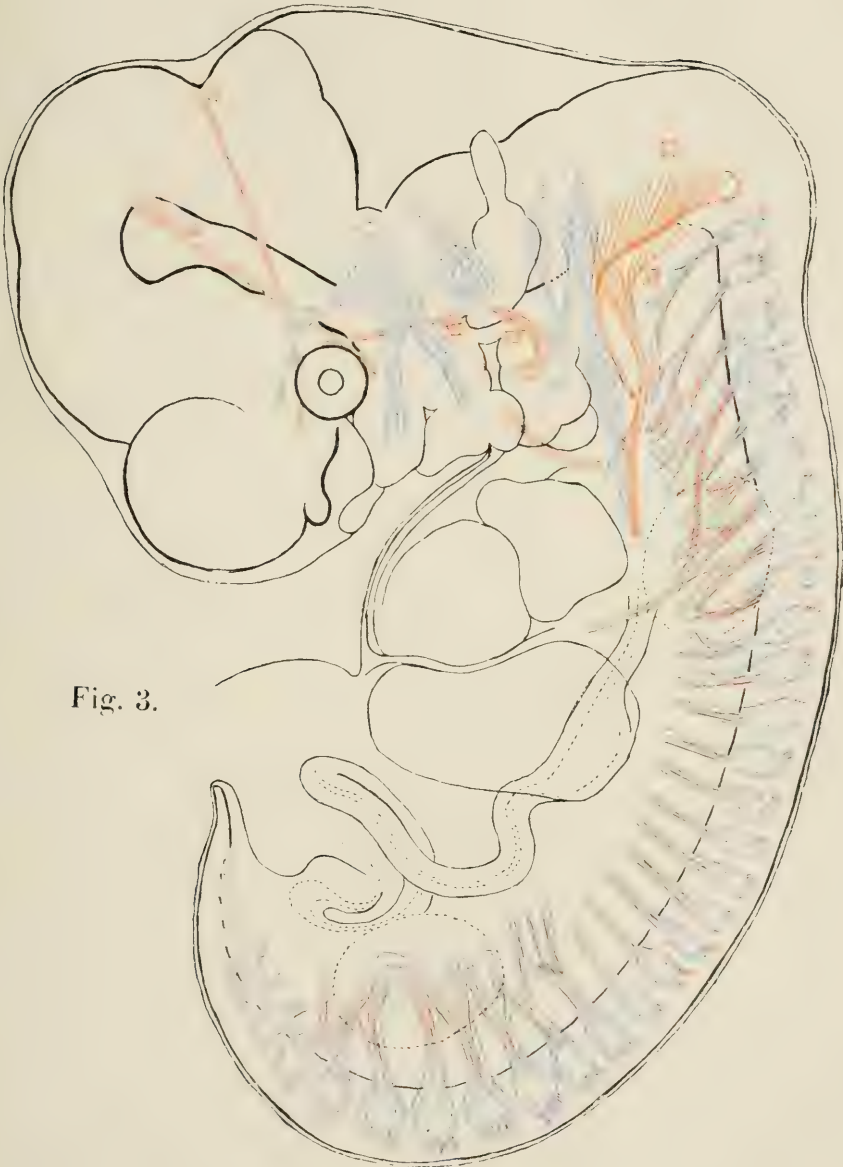


Fig. 3.







Fig. 4

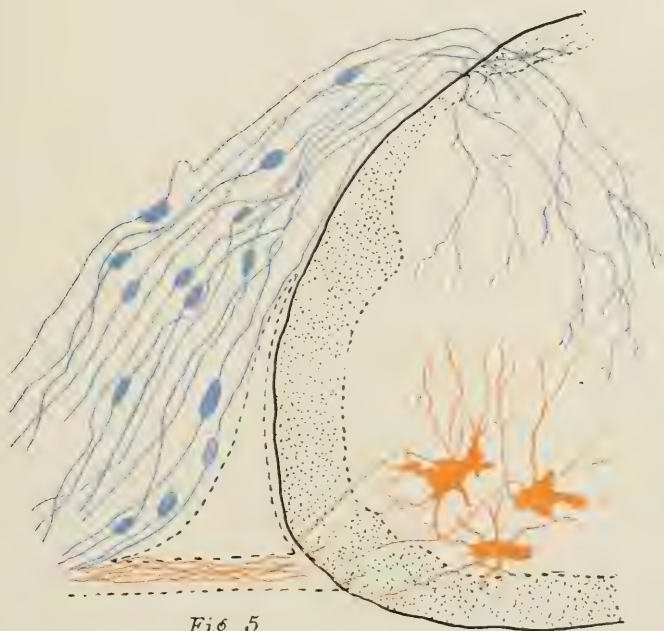


Fig 5



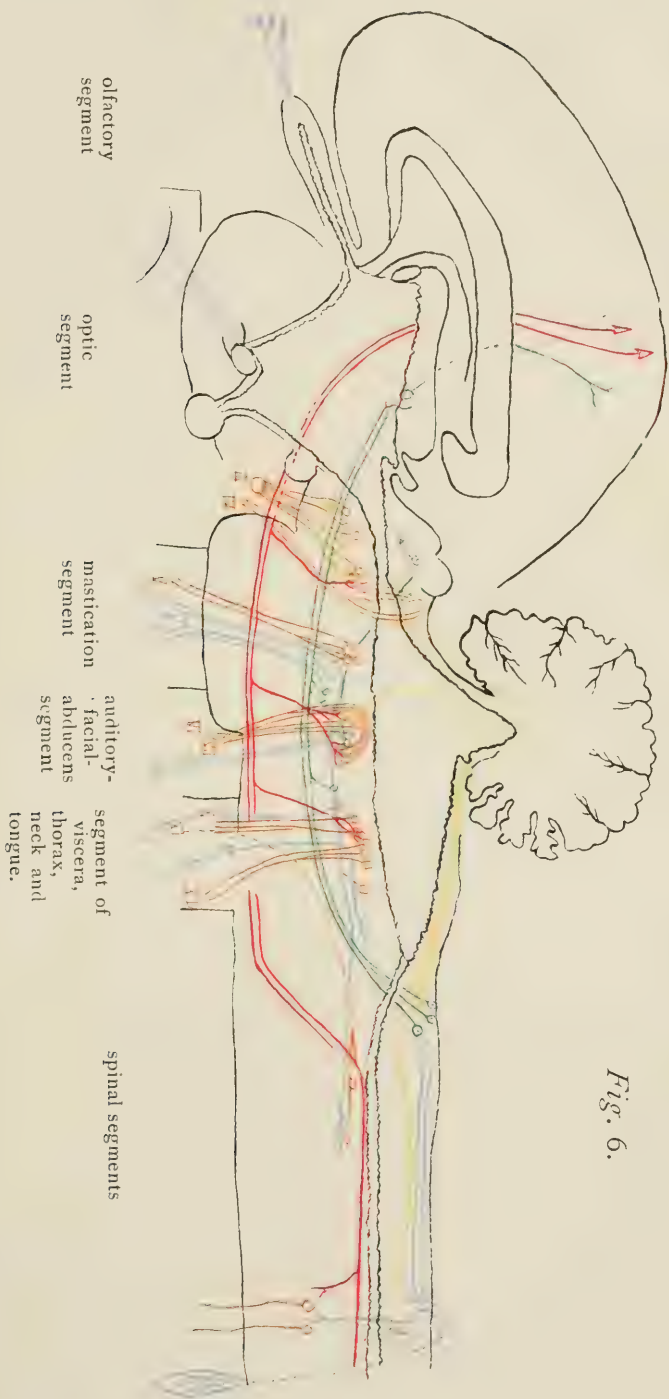


Fig. 6.





# CRITICAL REVIEW OF THE DATA AND GENERAL METHODS AND DEDUCTIONS OF MODERN NEUROLOGY.

By DR. ADOLF MEYER,  
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*Part II, With Plates XX and XXI.*  
(Continued from p. 148).

## The Nervous System as a Tissue.

Of all the tissues of the human body the nervous system is no doubt the least homogeneous one. Comparing one cubic millimeter of liver with another we would find for all we know now, the same oneness of liver-cells, of capillaries, of bile-ducts; there may be variations of size of the elements but not many types. The kidney may be a little richer in architectural forms and variations of the tissue-types—vessels and epithelia: or the lymph gland with its lack of architecture along hard lines of form has at least a sameness of principle and elements. The nervous system too has a certain homogeneousness. White matter compares easily with white matter; there are differences in the number of vessels, of various sizes of fibers and collaterals and the quantity and character of neuroglia and the manner of interlacing. But when we come to the ‘gray matter’ and its many shades passing over into ‘white matter,’ we get a great number of types, as our outline of the known neurone-types will make us expect: cells of great differences and therefore so characteristic for the locality in which they are seen.

Let us start in any section from a picture obtained with a nuclear stain and attempt to classify all the cell-elements. This task is by no means easy. To be sure, we know the well developed cell-types; but the transition forms? Starting with the mesoblastic tissue, we find the blood-vessels and their

sheaths, and in the sheaths or along them not infrequently cells, the real significance and derivation of which is by no means as clear as the term 'lymphoid-cells' would make one believe. Many 'lymphoid' elements of the literature are known to be neuroglia-cells. The satellite-cells, for instance, cells grouped around nerve-cells and especially increased in number in febrile and other processes, have repeatedly been called leucocytes, lymphocytes, phagocytes and what not, while it is fairly certain now that we are dealing with neuroglia-cells. On the other hand the cells in the blood-vessel sheaths are most frequently true cell-proliferations which are more properly derived from vascular tissues, not 'lymphoid infiltrations.' Next would come the various types of neuroglia and the nerve-cells. That there are in the adult any cells of a non-determined character, such as Schaper mentions in his study of the genesis of the elements of the nervous system, can hardly be doubtful, but requires definite proof. A study of the neuroglia with Mallory's or Weigert's method (or perhaps Robertson's?) is absolutely necessary for any valid statement on *these* structures, and the numerous problems concerning the nerve-elements call for methods for nuclei (Weigert, Heidenhain), for the Nissl-bodies (Nissl), for the fibrils (progressive hæmatoxylin stain, Graf, Bethe), the processes and their gemmules (Golgi), and finally for the various states of the fibers (Weigert, Marchi, Ehrlich, etc.) The composite picture of all these data will give us an accurate idea of the histological composition of a definite region. A sound pathological point of view demands absolutely that we look upon the object in the first line as a *tissue*. The general principles of nutrition and metabolism are only conceivable as related to a tissue, and only secondarily in an analysis of cellular units. This is easily demonstrated. The blood-supply is an all important index for the character of a tissue-type and on it depends the liability to special forms of pathological derangements. In this sense the vascular arrangement marks special forms of tissues. The other factor, closely related to the vascularity is the specific life of the 'parenchyma,' the nerve-elements. An interesting complication

arises because many nerve-elements are so large and spread into so many types of tissues, that a great variety of lesions must be considered; ischaemic necrosis may involve tissue with a *cell-body*, or only with a *dendrite* of one neurone or with the *fiber* or its *termination* and a simple lesion to a particle of tissue produces 'secondary' reaction in the 'outlying' part of the neurone. Another general fact deserves attention. A poison which is distributed by the circulation affects different elements of the tissue in different manners; and will even select different parts of the cell-individuals. We know, for instance, that the final termination of fibers and the myelin sheaths show a peculiar vulnerability to certain poisons (the metasyphilitic and the diphtheritic).

The general laws of interrelation of the chief constituents of the nervous tissues have been first outlined in a classical article by Weigert. (Weigert, *Centralblatt f. Pathologie*, Vol. I, p. 729). On the whole the following will represent the present status of the problem.

In the central nervous system there are three types of constituents of the tissues:

a. The nerve-elements proper, the highest type in the hierarchy both from the point of view of functional complexity and delicacy, and of difficulty of regeneration.

b. The neuroglia, also of epiblastic origin, but being less delicate and of the character of an interparenchymatous substance; part of it, many of the fibrils, are even put into the class of real intercellular substance (see page 129).

c. The blood-vessels, of mesoblastic origin, like the membranes (*pia*).

I am not aware of any peculiarity of the circulatory tissue-elements in the nervous system apart from the great tendency towards cell-proliferations, and pass over its general architectonic and pathological features. The claim of Hill and certain English students, that the blood-vessels of the brain are devoid of nerves has been invalidated by Obersteiner and I can adduce preparations to the same effect.



The nervous elements and the neuroglia have a most striking interrelation. In other organs we meet only the parenchyma and mesoblastic tissue, and one can recognize the general law, that a deterioration of the parenchyma finally leads to hyperplasia of the mesoblastic tissue; if a sufficient amount of tissue has become disintegrated without being regenerated a 'scar' forms, consisting largely of mesoblastic tissue which contracts and becomes more or less fibrous. In the nervous system, the (epiblastic) neuroglia takes a very prominent part in the repletory function, and the mesoblastic vascular tissue steps in more prominently only when both the nervous elements and a great part of the neuroglia have perished. Regeneration of nervous elements being a great exception, the neuroglia proliferation is the constant result of their decay. Attention has already been drawn to the importance of the general firmness of the tissue. In the new-born, the tissues are so plastic, that a defect is almost completely resorbed and the outline of the organ adapts itself to the defect; if, however, the form has become stable and more rigid, the filling-in is partly explained by the natural equilibrium of tension which must be established again if possible (compare the difference of neuroglia reaction in the spinal cord of (infantile) porencephaly and a secondary degeneration of the pyramid in the adult in Fig. 7. If the equilibrium of tension is disturbed too strongly so that collapse occurs before the gap can be filled up with neuroglia alone, a scar of vascular tissue plus neuroglia forms. This is the case where a disorder of nutrition destroys at once all the elements, so that an ischaemic necrosis of the entire district of a blood-vessel is established. It is not improbable that the occurrence of porencephaly and of lobar sclerosis is due to a very acute ischaemia in the case of porencephaly and a subacute or less complete ischaemia in the case of lobar sclerosis.

This compensatory relation between neuroglia and nervous elements does not, however, cover the only possible variations in the constitution of tissue-portions; indeed Nissl and Alzheimer insist very strongly on the observation that an increase of glia is possible without being a consequence of decay of

nerve-elements ; and acute degeneration in the cortex occurs in different disease-processes with or without an adequate neuroglia-reaction. Nissl has spoken of this same discrepancy in his discussion of the pathology of general paralysis. (Arch. f. Psych. Vol. 29).

The literature on the nervous system contains signs of numerous fluctuations in the views of the interrelations of these constituents of the nervous tissues. We mention as a mere curiosity the conception of Aristotle, for whom the blood-vessels contained the active spirit, while the brain tissue was merely a fat-lump to cool the excess of heat of the blood. In our enlightened age, there is an improved edition of this view to be found in a peculiar tendency of making the blood-supply responsible for, and not merely a help of, the activity of the 'nerve-cells.' As hyperaemia was long held to be the cause of inflammation, so Meynert has elaborated a remarkable system of hyperaemias and anaemias for the explanation of rest and activity of the nervous mechanisms and even for the explanation of disease-complexes. Further we see to this day two camps in the explanation of the pathological nature and starting point of general paralysis. To a large number of investigators the primary lesion seems the vascular alteration, while others follow rather the views which Weigert has formulated, according to which the parenchyma, the nerve-elements, are the sufferers and draw with them the neuroglia and the blood-vessels, A discussion of this burning problem would go far beyond my present task ; it is mentioned here in order to urge with more emphasis the absolute necessity of treating nerve-pathology as the pathology of a tissue and not merely a pathology of neurones.

Another wave in the same line is the view which Cajal has held for some time concerning the activity of neuroglia. Cajal's brother Pedro has pronounced himself in favor of the view that neuroglia serves to keep apart and isolate the nerve elements. Ramón y Cajal has observed that in an animal killed while asleep the neuroglia processes were longer and therefore 'isolated' better than in an animal killed awake, and on this

'activity of the neuroglia' he built a theory for the most complicated psychic activity.<sup>1</sup> This contraction and relaxation of the neuroglia may occur automatically or 'under the influence of the will' [!] just as the blood-vessels under Meynert's plan. These two views should be enough warning against taking to the third possible one-sidedness, namely to the idea that movements of the nerve-cells alone constitute nervous activity.

We do well to consider the activity of the whole tissue when we speak of the function. In the meantime it will of course be our duty to analyze carefully the possible share of each tissue-element, in order to be prepared for a final summing up.

These considerations seemed necessary as an introduction to a sketch of what we know of the life of certain kinds of nerve-cells. They must be borne in mind in the following discussion and especially when we begin to speak of the diseases of the nervous system. The life and pathology of the neurones to which we must limit ourselves here, is by no means a complete pathology of the nervous system.

### The General Physiology and Pathology of the Neurone.

Any one who takes the trouble to examine many nerve-cells belonging to the different mechanisms described, will admit that there are many fairly characteristic forms. The old method of classifying nerve-cells as unipolar, multipolar, etc., has been modified, and more definite details of structure and outline of form have been used for the classification since the methods of Golgi and Nissl have rendered them easily demonstrable. Nissl himself has furnished a plan for the classification of nerve-cells which is somewhat too complicated to be given in full here. I shall prefer to give here a short sketch of certain cells which are of importance for us in the general plan of the nervous system, since only few types are sufficiently studied to

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<sup>1</sup> Cajal, *Algunas conjeturas sobre el mecanismo anatomico de la ideacion, asociacion y atencion*. Madrid, 1895.

allow definite statements from the point of view of pathology and of entities.

1. The motor neurones. To begin with, we must admit that it is impossible at present to examine wholly one entire motor neurone in the adult on account of the length and irregular course of the processes, and our inability to isolate it completely or to get the whole into one plane. The Golgi impregnations do not give as perfect results here as in other cell-types. The cell-types given in Fig. 5 are quite characteristic. It would not, however, be possible to recognize from the outline alone that the cell was motor except when the axis-cylinder going into the nerve could leave no doubt. The Golgi 'stain' gives a uniform black color to the cell-body and the processes.

In reality, we depend in our studies mostly on the stain of the cell body with the Nissl method and on the Weigert stain for the medullated fibers. We give up the attempt of staining all the parts of the cell at once in order to obtain more characteristic details. When speaking of disorders of the whole motor neurone, we do so always making an abstraction from a composite picture. We are forced to study one entire nerve or many nerves and muscle-endings in corresponding segments of the neural tube and from the sum of results we *abstract* the probable picture of entire neurones. Many points derived from histological and experimental experience are tacitly understood in this process. It would be impossible to demonstrate to a person without any knowledge of the subject that certain cells are in connection with certain muscles except by a whole series of collateral observations. On ground of a number of experiences, we have learned to recognize cells which invariably are connected with certain muscles. This is for instance done with perfect satisfaction in the case of the abducens or trochlear apparatus of the eye, where one group of nerve-cells, one nerve and one muscle only enter into the formation. In the facial or hypoglossal nerve we have one group of nerve-cells, one nerve and several muscles; in the oculo-motor, several groups of nerve-cells, one nerve and several muscles, and in the spinal nerves we know that one muscle receives as a rule fibers from



several spinal nerve roots. These form a plexus where the fibers join which belong together. The cell-bodies for one muscle of the spinal segments are usually scattered through several segments. In the facial, abducens and hypoglossal nuclei we find the cells of one type grouped together and the intermediate cells (for the ground-bundles) very probably outside of the group, in the reticular substance; in the spinal cord the motor cells are less closely grouped; the intermediate cells are to some extent scattered among them. The best places for a study of the cell-bodies of the motor neurones are therefore the cranial nerves mentioned, the best one of all the abducens, because there is hardly any objection to be met to the trio: one nest of nerve-cells, one nerve and one muscle. This apparatus is studied and pictured by von Gudden (Abhandlungen, Plate XL, Fig. 11). In the following I shall refer to the hypoglossal motor neurones, partly because of the possibility of referring to the figures of Forel, partly because I make use of material obtained experimentally by myself. We see large cells forming a group on either side of the raphe in the floor of the fourth ventricle within its posterior segment (behind the point from which the *striæ acusticæ* emerge). From these 'nuclei' bundles of fibers arise which run at first parallel to the raphe and then leave the medulla between pyramid and olive, to form the hypoglossal nerve, which can be followed into the muscles of the tongue.

It is our first duty to prove that these cells are really all in connection with the fibers mentioned and that all the fibers of the hypoglossal nerve come from these cells. The evidence is furnished in the description of Forel and of my own Nissl preparations. Forel *tore out* the hypoglossal nerve in a new-born guinea pig. The animal was allowed to grow to adult age and was then killed. Regeneration of the peripheral nerve did not take place (as is always the case when the entire nerve is *torn out* in the new-born). Not only had regeneration not occurred; but the neurones which could not *regenerate*, *degenerated* completely. Fig. 8, represents the central canal and surroundings of the lower part of the medulla oblongata of this animal. On the right side, the large cells described above as

hypoglossal nucleus are present in normal number and size, and fibers come from it which constitute the hypoglossal root. On the left side, these *fibers* are absent and also all the *cells* of the nucleus. The two nuclei of the pneumogastric are normal and symmetrical, and also the small celled nuclei of Roller along the ventral border of the hypoglossal nuclei. Therefore, they do not belong to the hypoglossal nucleus. This is one part of our evidence. Another point of evidence is obtained by a simple section of the hypoglossal nerve before it enters the tongue, in an adult animal which is allowed to live two or three weeks. The hypoglossal cells of the side on which the nerve was cut, all show a peculiar alteration with the Nissl-stain. In order to understand the change we must proceed to describe the 'equivalent' of a normal hypoglossal cell as obtained by the method of Nissl. The hypoglossal cell has a large nucleus with large nucleolus, located near the center of the cell. The nuclear membrane is rarely visible, being covered up by characteristic lumps of stained substance which are arranged in a typical manner within the cytoplasm and the dendrites, more or less compact portions of a stainable substance being separated by channels of non-stainable substance, more or less parallel to the outline of the nucleus and also to the outline of the cell-body and largely longitudinal in the dendrites. In a few of the cells, the section exposes a small area on the surface which contains no stainable lumps and from which a faint process arises, the neurite, free of stainable substance. On the normal side of our section the cells all show this arrangement although in the detail of outline of the cell, form and size of the 'granules' and presence or absence of the nerve-cone the individual cell-pictures vary greatly. On the side on which the hypoglossal nerve was cut, the cells show a peculiar change. At first sight they appear swelled and more diffusely stained than those of the normal side. The stainable substance is in a process of decay and covers up the channels of non-stainable substance. The nucleus becomes more visible, its membrane is no longer covered up by the lumps. Other cells show a marked swelling and the center is taken up by a more or less glassy slightly dusty tissue

which pushes the nucleus towards the periphery of the cell-body and even beyond the normal outline so that it projects. At the same time the outline of the nucleus loses the round shape. The dendrites are somewhat less involved, but also a little diffusely stained. A good illustration of this condition is furnished in a paper on facial paralysis by Dr. Adolf Meyer, in the *Journal of Experimental Medicine*, Vol. II, No. 6.

There remains to be said that the cell recuperates as the regeneration of the fiber takes place and that the cell atrophies if no regeneration can take place or especially where the fiber is torn or cut off close to the point of exit from the neural-tube. (This explains the bad prognosis of 'radicular' paralysis.)

In this manner we have not only established the physiological connection between the cells of the hypoglossal nucleus and the hypoglossal nerve but some important laws concerning the neurones. The Golgi stain gives evidence in a few of the cells that the axone extends into the hypoglossal root. The above method shows that *all* the cells react in the same way to injury of the nerve and the conclusion is safe that all the cells which show this change are hypoglossal neurones. That the peripheral stump of fibers of a cut hypoglossal nerve degenerate has been shown by Waller and many investigators after him; that the same injury affects the cell-body as well, is demonstrated by Nissl; Bregman has also shown that tearing out of a facial nerve in an adult guinea-pig is followed by a partial degeneration of the central stump of fibers (demonstrated by Marchi's method), in which case the degeneration of the fibers goes hand in hand with deterioration of the cells. And in the new-born this 'atrophy' and degeneration are complete, ending in resorption (v. Gudden, Forel).

All these data are in perfect harmony with the consequences of the neurone-theory. The cell-body is the vital focus of the neurone. Not only do the processes die when cut off from it, but the cell-body is influenced by an injury to the neurite and if the greatest part of the neurite is cut off, the cell is subject to atrophy and perhaps even to complete resorption. The fact that the reaction is limited to the neurone and does

not involve other cells speaks in favor of an histological independence, but would not prove it absolutely, nor does it throw any light on the actual mode of interrelation of neurones without special microscopic investigation in just this direction with especially delicate methods.

Dr. Becker in Rastatt was able to stain a few of these cells with a method which does not seem to give constant results and has not been published. Nissl gives a photograph of one of his preparations in the *Allg. Zeitschrift für Psychiatrie*, Vol. 54, plate II, Fig. 4, which demonstrates that it is possible to isolately stain fibrils in the motor cells not unlike those described long ago by Schultze. 'The fibrils run through the cells and processes as a rule in small bundles; a small number consists of isolated fibrils. Both the individual fibrils and the cables of fibrils take by no means always a straight course; they form large circles around the nucleus instead of following a straight line. The reason for this is not clear. For the proof that the non-stainable substance carries these fibrils the course of the fibers in spirals of the greatest importance.' 'This leads to decussions of all kinds. One portion of all the fibrils does not seem to enter the cell-body at all. Such fibrils and fascicles enter by one process and leave again by the next one. In this case they run along the neighboring surfaces and describe the figure of an U. A difference between the dendrites and neurites could not be established. The fibrils never penetrate the wall of a nucleus. They always pass it. (Kronthal-Thannhofer's method shows fibrils entering the nucleus and even nucleolus, but according to Nissl these findings are fibrils of stainable substance artificially produced while Becker's fibrils have nothing to do with the stainable substance). Apart from the motor cells no other nerve-cells have shown this structure. It is especially important to note that a cone of origin of the neurite cannot be demonstrated in the Becker cells. This implies that the non-stainable substance consists of at least two constituents, fibrils and another substance.' The great difficulty is now the explanation of these fibrils and their relation to the cell-body. Nissl mentions three possibilities: either the fibrils



originate in the substance of the cell-body, or they do not originate in the cell-body, or there are fibrils which originate in cell-bodies and others which originate outside of the cell-body. He goes as far as to say: 'it is therefore quite possible that there are cells which originate purely fibrils and others, through which fibrils take their course without there arising any fibrils in them.'

The fact is that we have no idea at present where these fibrils originate, and it is this consideration that led me to see a possible complication of the neurone-theory in analogy with the results of Weigert's neuroglia-theory. As far as we can see now there is, however, only a logical similarity, not a similarity of fact in the two questions. In the neuroglia, Weigert sees fibers independent of cells and where they are in connection with cells they simply *pass* through the protoplasm. The Becker-method produces fibrils within the 'protoplasm,' but Nissl is unable to see fibrils originate in the cell-body; he suggests that they might originate in the dendrites; but he also says (page 64): 'it is also easily possible that there are cells which merely give origin to fibrils and others through which fibrils take their course without there arising any fibrils.' This leads to complications which will only be cleared up when a good method for the nerve cell fibrils is available, such as Bethe is said to have discovered.

That the axone or neurite contains fibrils is admitted by most writers now. Held and Lenhossék admit this but deny the view that they are continued beyond the cone of origin of the neurite into the cell-body. It is almost useless to discuss this matter in connection with the motor element. It seems that Becker's evidence is strongly in favor of fibrils not only in the axone but also in the cell-body. We shall return to this in the discussion of the afferent neurone, and when speaking of the latest publications of Held.

The stainable substance seems to be more akin to a nutrient plasma than to a substance specially important for nervous function. The remarkable finding recorded by Nissl (*Allg. Z. f. Psych.*, Vol. 54, p. 67), where an invasion of just the stain-

able substance by cocci had occurred while the other tissue, except the blood-vessels, was free from cocci, is very suggestive.

During the process of repair after section of a nerve, Marinesco (*Comptes rend. de la Soc. de Biol.*, 1896) has found gradual re-formation of the Nissl-bodies from the twenty-fourth day; even ninety days after the section the cell shows a hypertrophic condition, probably a sign of the effort of repair of the nerve. (A pyramidal cell in this condition is probably Fig. 4 of Meyer's demonstration, *J. of Insanity*, 1897.) Whether pigment is apt to remain, as the drawing of Meyer (*Facial paralysis*, *J. of Experimental Medicine*, Nov. 1897) would suggest, is uncertain.

Fibril stains have not been published in this important reaction. All we know is the alteration of the trophic substance and the fibrillary substance remains to be studied.

Apart from the traumatic reaction many other alterations have been observed in the cell-bodies of motor neurones. Marinesco has established a view very widely accepted, that the 'traumatic' lesion (the reaction to an injury of the fiber) is one of the center of the cell with dislocation of the nucleus to the periphery; while the primary lesion of the cell (toxic, anaemic etc.) begins with the chromatolysis in the periphery of the cell.<sup>1</sup> This does indeed justice to the ordinary demands; but more accurate study calls for a further classification of the 'primary' lesions of the cells. It would lead us altogether too far away from our subject to enter here upon a review of all the work of Nissl and his followers since Goldscheider's important study will give us all the principal data for the neuro-pathological discussion. I restrict myself here to the statement, that the chromatolysis may proceed in various fairly typical manners, that the achromatic substance begins to take the stain, that the nucleus becomes altered and that the degree of alteration of the nucleus has been recognized by Nissl to be

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<sup>1</sup>Des polynévrites en rapport avec les lésions secondaires et les lésions primitives des cellules nerveuses. Par Georges Marinesco. *Revue Neurologique*, Vol. IV, pp. 129-141. With 7 drawings.

the guide as to the ability to recuperate. When the nucleus begins to be homogeneous, deeply stained, round or oval, but smaller, finally losing the capsule, so that it lies in an area of light plasma, Nissl speaks of the grave alteration indicating the fatal disorganization (Z. f. Psych. Vol. 54, p. 47.). There are a number of facts which force me to leave this point undecided and not to join Nissl in his verdict, but this does not belong here, being of no fundamental importance for the neurone-theory. It is a detail-question, how far the nucleus must be altered to lose the power of recuperation.

It will hardly be necessary here to rehearse the processes of degeneration and regeneration of the peripheral motor nerve-fiber. Only the following data seem to be worth special attention:

1. The most vulnerable part of the fiber is the final termination in the end-plate (Gessler), then the axone and next the medullary sheath. The latter being most accessible to rough methods shows the alterations readily.

2. Notwithstanding constant revival of the 'growth of axones in the nerve-end which was cut off,' we can trust competent investigators who say that the regeneration of the axone always proceeds from the cell or at least from the stump which remains in connection with the cell.

3. The 'trophic function of the anterior horn cells' is no special trophic function for the fiber but a necessary side of the cell-theory. It is evident that a process of a cell depends on the integrity of the nucleus and cell-body. The relation of the muscles-fibers and the neurones governing them is however a trophic relation between the *entire* neurones and the muscle-fibers. Whether the neurones be affected in the cell-body or in the fiber or termination, does not influence the mode of alteration of the muscle. The latter depends on the activity and condition of the motor neurones as a whole.

For the appreciation of the life and activity of a segmental afferent neurone, I add the results of an interesting study of

A. Beck.<sup>1</sup> Beck chose nerves which did not contain any centripetal fibers which might have excited the muscle of the experimental nerve by the way of a reflex; he isolated the nerve for a long distance and applied an induction current just strong enough to obtain a minimal contraction. He found that the current had to be stronger the more centrally he excited the nerve. The same result was obtained when he used an accurately gauged galvanic current. While, of course, stimulation is far from being the same as genuine neural activity, the experiment would vindicate a greater independence of the fiber from the cell as far as function is concerned, than for nutrition and vitality and this experiment might be adduced as a starting point for investigations by those who see the neural unit in the fibril, not in the cell, unless we should be able to prove that the fibril is merely a conductor of the *electric* current and the contraction of the muscles a result of this electric stimulus. In this case the result of Beck's experiment would be just what one would require, and nothing would be gained from it for the activity of the neurone.

Gowers, in the *Dynamics of Life* (London, 1894) stands on this ground and urges (p. 37) that neural energy is generated in the fibrils of the spongy substance, not in the cell-body. For him, the fiber is generator and conductor. While in this and the subsequent discussion I pass over this view, I think it but fair to mention the above experiment of Beck as a possible element of discord for the future.

Another suggestion made by Onufrowicz in the *New York Hospitals Bulletin*, 1897, would deserve notice here as a future problem. He assumes that the inhibitory influence of the pyramidal tract is obtained not by a contact of the cerebral efferent (indirect motor) neurones with the cell-bodies or dendrites of the segmental motor neurones, but only with the *collaterals* of the axone of these neurones. Ingenious as this may be, it is mentioned here merely as a possible problem for the future.

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<sup>1</sup> A. Beck, Die Erregbarkeit verschiedener Stellen desselben Nerven. *Arch. f. Anat. und Phys. Phys. Abt.*, H. V. and VI, 1897.



2. *The segmental afferent neurones.* The cells of origin of the afferent neurones are grouped together in the spinal ganglia and the ganglia of the afferent cranial nerves. The olfactory afferent neurones belong to the type described as modified epithelial cells (see the description of the nervous system of *Lumbricus*); in the *Amphioxus* there is a third type inasmuch as the sensory neurones have their cell-bodies within the spinal cord. It is possible that the midbrain-root of the fifth nerve belongs to this category. Both these types cannot come into question in this general study.

Since Flemming gave his classical description of the spinal ganglion cell, many important studies have come forth. Especially the important experiments of Hodge were made on them; further we have detailed descriptions by v. Lenhossék, Held and Nissl. We start with the description of the cell-body as it presents itself with the Nissl method. The cells of this type (see the drawing by Nissl, *Neurolog. Centralblatt*, 1894, and also the plates of v. Lenhossék, *Archiv für Psychiatrie*, Vol. 29, Taf. VI and VII) are round or oval, with only one nerve-process in the human adult, but two in the embryo. The nucleus is located near the center, with a plain membrane and moderately large nucleolus. The stainable substance consists of smaller lumps than in the motor cells; they vary greatly in size and distribution, so that Nissl is obliged to describe several 'equivalents' or types. The larger particles are usually concentrically arranged either close to the periphery or further towards the nucleus in one or more 'layers;' smaller particles give a less clearly concentric arrangement. The larger particles appear usually composed of smaller ones and are not homogeneous. The non-stainable substance is also more or less concentrically arranged but not in as plain paths as in the motor neurones; in many cells there is a superficial layer quite free of stainable substance. Where the axone arises there is a plain cone of origin, free of stainable substance.

The principal discussion has turned around the character of the non-stainable substance. Held and Lenhossék (quite recently, however, Lenhossék has expressed himself in a

discussion as being convinced of Flemming's view, especially by Lugaro's sections, just to be mentioned) deny its fibrillary structure, but it seems that Flemming's view is very emphatically substantiated by the Italian investigators Levi and especially Lugaro.<sup>1</sup> The studies of the latter are very important for us. He found that a progressive stain with Delafield's hematoxylin brought out plain fibrils in the non-stained substance all through the cell; further that certain intoxications which lead to a reduction of the stainable substance bring out very clearly these concentric bundles of fibrils; and finally that the reaction of the cell to injuries of the processes follows this rule:

As a consequence of a lesion of the *peripheral branch* of their neurite the spinal ganglion cells undergo a process of alteration which may lead even to the death and to the disappearance of the element; whereas they preserve their normal structure when the *central branch* is cut off. The process of change in consequence of section of the peripheral branch is identical in character with the one described for the motor cells (see Lugaro's Fig. 7). This furnishes the explanation for the puzzling fact that in locomotor ataxia but few alterations or none are found in the cells in the spinal ganglia; further it is of importance for the formulation of the laws of trophism of the nerve-cells generally.

This would be the place to pass in review the important results of investigations of Hodge and others on changes in fatigue and intoxications, but this lies outside of our present task. We shall mention them in the general pathology.

Apart from the study of ordinary degeneration of the peripheral fibers and the coarse central branches and also of the histology of peripheral and central terminations of the afferent neurone in the normal, little is known outside of the pictures obtained by the Golgi method. The best is undoubtedly what we know from Monakow's studies of the primary optic

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<sup>1</sup> Sulle alterazioni delle cellule nervose dei gangli spinali in seguito al taglio della branca periferica o centrale del loro prolungamento. Ricerche del dott. E. Lugaro, assistente. Rivista di Patologia nervosa e mentale, Vol. I, p. 457-470.

centers, Mayser's description of the lesions of the spinal cord experimentally produced, and above all the wonderfully clear results of Forel shown in Fig. 9. The specimen represented there is a section from the medulla oblongata of a guinea-pig in which the right pneumogastric had been pulled out soon after birth. The consequence was degeneration of the segmental motor neurones of the tenth and also of the segmental afferent neurones, which have their cell-bodies in the jugular ganglia; all the cells of the motor tenth are atrophied and degenerated, and all the cells of the 'sensory nucleus' have moved more closely together. On the healthy (left) side, these cells are separated by broader spaces of ground-substance or 'spongy substance.' The end-arborizations of the afferent neurones of the tenth nerve form part of this spongy substance and their degeneration brings about a considerable reduction of the spaces. An instance of the conditions following a lesion of the auditory segmental afferent elements is quoted further on. The whole connection between the afferent and efferent and intermediate neurones is rather a matter of schematic illustration than of accurate histological knowledge. Special affections of the reflex-collaterals and the fibers to the columns of Clarke, and further early degeneration of the thin root-fibers (Lissauer's zone) have been described in tabes, but they are neither correlated with cell-bodies of special character nor with sufficiently well isolated functions in the clinical picture.

Van Gehuchten calls the peripheral branch of the neural process a dendrite and the central branch a neurite, probably in order to save the general doctrine that the 'current' or impulse is carried from the end of the dendrite through the cell-body to the axone. This seems to be against the facts revealed by Lugaro. The general *law of conduction*, as just stated, must probably be sacrificed. The section of a peripheral nerve producing exactly the same lesion in an afferent and in an efferent neurone, puts them on equal footing as neurites (axones) and if one fiber is to be identified with the name dendrite, it is undoubtedly the one which ends in the neural tube, both on account of its numerous ramifications and the peculiar

relation to the cell in case of degeneration. In numerous cases of tabetic degeneration which I have examined the negative experimental result of Lugaro after section of the posterior root-fiber is fully corroborated: the spinal ganglia show practically no lesion. Apart from the absence of a necessity for forcing general laws when they do not fit with the facts, we do best to recognize in the segmental afferent neurones a cell-type essentially different from the motor in development, mode of conduction and pathological reaction. It is not improbable that among the 'central' cells we shall ultimately find similar or other types which do not fit into the general pattern of a 'motor neurone.' I merely suggest here the peculiar origin of the thalamo-mammillary and the mammillary-tegmental tract discovered by Cajal, and the fibers of the corpus callosum which need study before we formulate *the* law of the neurone.

*The intermediate neurones* are very poorly known. Hoche has shown that, in the spinal cord segments, the fibers run closer to the gray matter the shorter they are, and further towards the surface the longer they are; further, studies of Bruce and others have demonstrated that the anterior ground bundles are more especially in connection with the anterior horn, the lateral ones with the lateral, etc. A detailed study of types of intermediate neurones will only be possible when the cells belonging to the supersegmental mechanisms are more strictly ascertained. We shall then be able to find out by the way of exclusion just what the intra- and inter-segmental neurones are. The conditions are naturally more difficult in the cranial segments on account of the complexity of their functions and the presence of the supra-segmental mechanisms, cerebellum, midbrain and basal ganglia. The simple plan given in the chart of the architecture does not include many anatomically well-known entities because their functional relations are in no way elucidated yet.

In the literature of the Nissl stain we come frequently across the term: 'cell-structure of the motor type.' It would correspond with Nissl's 'stichochromous type,' the cells in which the stainable substance is arranged in lumps or spindles



which leave straight or spiral-shaped canals for the non-stainable substance which carries the fibrils. It would be a grave error to see in the structure anything characteristic for anything 'motor.' We have no real knowledge of the difference of the neural activity in afferent and efferent elements. If we call the one 'motor' it is only justified on account of its connection with a muscle. There are indeed cells of stichochromous type in the medulla oblongata—the large cells of the reticular substance, and also the cells of Deiter's nucleus, which are certainly not motor in the sense that they would go to muscles, but it is not improbable that they terminate around real motor neurones and have the character of inter-segmental neurones for the motor elements. There are similar cells in the spinal segments, and it would be decidedly unwise to think that from the structure of the cell-body alone we would be able to read its functions. This stage of neurological knowledge is not yet reached.

3. *The cerebral afferent neurones.* The cerebral mechanisms have been studied with more persistence than any other part of the nervous system since the so-called cerebral localization did away with the diffuse and misty views of Flourens. Nevertheless our actual knowledge is yet far from being a knowledge of neurones and of their accurate connections.

Even those who work more especially on the cerebral cortex, will have to admit that the knowledge of the cortex stands in its very infancy. Conjectures are certainly numerous; there is also no lack of description of layers and, lately, even of cell-types; also medullated fibers have received their share of attention; but neurones? cell-bodies with all their processes and terminations? We are just approaching an almost perfect knowledge of a few types of elements and the best known simple elements (Cajal's cells) are least knowable as to their functions. This may be the reason why von Monakow, one of the best investigators of the nervous system contents himself with a description of the 'gray matter' and the 'white matter,' just as of olden times when a fiber did not call for a cell with ab-

solute necessity, nor 'white matter' for groups of cell-bodies, to make a description intelligible in terms of neurones.

This state of things is to be attributed to the almost exclusively histological study of the normal cortex and the scarcity of systematic experimental work on the various layers and cells. Apart from v. Gudden, v. Monakow<sup>1</sup> and Moeli<sup>2</sup> there are no investigators known to me who paid due attention to this point. The only illustrations of the matter in question are to be found in v. Monakow's studies, e. g. in his *Gehirn-Pathologie*, p. 264 and 265.<sup>3</sup>

The known entities of physiological importance are:

(1). The *cerebral afferent neurones*. In our plan of the brain we find the majority of the cells of the nuclei of Goll and Burdach send their axones into the fillet of the opposite side. The fillet, at least the cerebral or median fillet (the midbrain fillet comes largely from the auditory segment and from the scattered cells of the cord which help to form Gowers' tract—Monakow and Mott), has been traced with certainty up to the ventral nucleus of the thalamus, where it ends.<sup>4</sup> Fresh neurones have their cell-bodies there, but that they send their processes to the motor and parietal areas of the cortex is only indirectly known through the extirpation experiments of v. Monakow. A minute description of the cell-body of the fillet-neurone does not belong here, because it has no pathological importance yet. Only two points need be mentioned, viz.: that the cell-body varies much in outline and size and that its stainable substance consists of small to medium sized granules, not always plain. I have not infrequently found cells with loss of

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<sup>1</sup> Du rôle des diverses couches des cellules ganglionnaires du girus sigmoïdeus du chat. *Arch. des Sciences phys.* Genève. Vol. XX, 1883.

<sup>2</sup> Ueber Degeneration der Hirnrinde nach Zerstörung der Faserung der Capsula interna. *Berlin. phys. Ges.*, 1. Febr., 1883.

<sup>3</sup> See further: Carlo Cani, *Sulle fine alterazioni della corteccia cerebrale consecutive alle lesioni della midolla spinale*. *Riv. di Fren.*, 1896, XXII, fasc. I.

<sup>4</sup> Flechsig and Hösel claim that at least a great part of the fillet runs to the cortex without interruption in the thalamus. But so far nobody has corroborated them with a conclusive method.

granules and eccentricity of nucleus when I could not find an obvious traumatic lesion of the neurites. Whether all the cerebral afferent neurones for the spinal segments have their cell-bodies 'centralized' in the nuclei of Goll and Burdach, and which cells of the nuclei of afferent cranial nerves are cerebral afferent and which ones are simply 'intermediate' is hardly possible to say now; nor is it certain whether we can distinguish the *cerebellar* afferent neurones from them simply by a study of Nissl specimens. The external nucleus of Burdach is most probably a pure cerebellar 'Anteil'; but there is no marked peculiarity of its cells, except perhaps in their greater resemblance with those of the nucleus lateralis, in size as a whole and of the granules.

We have seen that the *cerebral* afferent apparatus consists of two sets of neurones, one terminating in the thalamus and one arising there. This same plan holds not only for the common sensory-motor cerebral apparatus, but also for the visual-motor and the other special mechanisms. Since the optic apparatus is the best known, it may find a place here especially because in its literature we find splendid illustrations of general and experimental pathology.

The retina consists of three layers of neurones: 1. The rods and cones, 2. the intermediate layer, and 3. the ganglion-cell layer; between the first and the second and the second and the third, there are 'molecular layers,' i. e. tissue composed of the end-fibrils of the cells of these layers. The ganglion-cells give rise to fibers which help to form the optic nerve and tract and terminate in the external geniculate body, the pulvinar and to a lesser extent, in man at least, the anterior corpus quadrigeminum. Among the cells located among these 'primary terminations' there are some which belong to the cerebral afferent neurones; especially most of the cells of the external geniculate body belong in this category; their neurites form the 'optic radiation' and terminate in the visual area. We saw in the introduction<sup>1</sup> the very interesting differences of degener-

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<sup>1</sup> See p. 118.

ation of the external geniculate body according to whether the eye or the occipital cortex is removed, and that this finding is interpreted by Forel in favor of his neurone-concept. If the eyes are removed, the end-arborizations of the optic nerve fibers in the 'ground-substance' of the external geniculate body will decay; consequently the cells will come more closely together, part of the ground-substance being resorbed; if however the cortex is destroyed the optic radiation is affected and its cells will undergo atrophy and even resorption and neuroglia forms the scar. (See Monakow's *Gehirnpathologie*, Fig. 82 and 83). We must remember that the resorption is most complete where the lesion occurs in very early life. The general law is easily demonstrated in the spinal cord of cases of infantile hemiplegia where the degenerated direct pyramidal tract is often resorbed without leaving a neuroglia scar, and the area of the degenerated crossed pyramid is very much smaller than in the case of hemiplegia in the adult or senile.

(2). Among the *cerebral efferent* neurones we really are familiar with the pyramidal systems only. The thalamic radiation and even the efferent paths to the cranial nerves are not accurately enough known to allow us to speak of complete neurones, although the latter have been much cleared up by Hoche. All bodies of the efferent '*motor*' neurones belong to the pyramidal type, a cell-form which undoubtedly owes its outline to the peculiar composition of the cortex in layers with more or less perpendicular radiation of fibers. Among the many forms of cortical cells the large motor pyramidal cells are quite characteristic, not only by location but by structure. These are the ones which von Gudden and von Monakow have shown to be absent after destruction of the internal capsule in the young.

These large cells of the motor region are located in the deeper parts of the fourth layer of Cajal; the most striking ones are the giant pyramids of the paracentral region, between the layer of small cells and the polymorphous. They are among the largest cell-bodies of the human nervous system, perhaps because a correspondingly long neurite comes from them. The



form is usually pyramidal although it is difficult to always strike the right plane for making sections; a deviation from it produces pictures like the real motor neurones in the ventro-lateral lamina of the neural-tube. To judge from numerous specimens it would, however, be wrong to say with Nissl that they were not pyramidal.

In structure, they represent the 'motor' type. The large lumps of stainable substance are regularly arranged, leaving plain paths for the non-stainable substance which contains the fibrils. The apex-process and the lateral processes have a very neat arrangement of longitudinal spindles. The nucleus and nucleolus are very large. A number of drawings which lately appeared in the *Journal of Insanity*<sup>1</sup> give a fair idea of both the normal and certain abnormal conditions of this type of cells, at least figure 1, 4, 6 and 7. The writer describes several alterations of the cell-body; for Figs. 3 and 4 he urges the probability of a lesion of the neurite, for Fig. 6 and 7 toxic processes; but we necessarily miss statements concerning the fate of the fiber-part of the neurones, since it would be impossible at present to study their fibers thoroughly in their whole extent; the real terminations of the pyramidal fibers especially being only little known, and no methods for their isolated study being available. The efferent cerebral neurones which are not a part of the pyramidal system are comparatively little known. Apart from the studies of v. Monakow and Moeli there are very few data, and even these are hardly sufficient to establish any satisfactory description of these *neurones*. There are many well founded suppositions; but suppositions are not neurones.<sup>2</sup>

There are quite a number of intra- and inter-cortical nerve-elements, cortex-cells of which we might give descriptions here,

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<sup>1</sup> Demonstration of various types of changes in the giant cells of the paracentral lobule, by Adolf Meyer, M.D. *American Journal of Insanity*, Vol. LIV, No. 2.

<sup>2</sup> Through an oversight the cerebral efferent supply of the third, fourth and sixth nucleus is represented in the 'plan of the brain' as coming through the pyramids. It is more probable that the origin of these elements lies in the large cells of the visual area and that their course is independent.

further the cell-types of the cornu ammonis etc. The cell-bodies are very eagerly studied now both by the Nissl school and the friends of the Golgi method. It is by no means an easy task to correlate the two series of results, because the gemmules, very striking parts of the Golgi pictures, are but rarely reproduced by other stains.

3. The study of the cerebellar mechanisms has received a new stimulus through the application of the methods of Golgi and of Marchi. The field is, however, still full of contradictions. For the plan of the brain I should accept the sketch of Thomas,<sup>1</sup> since my own investigations on this point are not yet sufficiently advanced. Only few of the elements which unquestionably belong to the cerebellar apparatus are known so as to be pictured as neurones on ground of actual demonstration. We take up only the best known elements.

Since Flechsig's investigations, the direct cerebellar tract is known as the principal afferent system of the cerebellum from the spinal segments. The cells of Clark's column are considered to give origin to it. They have a fairly characteristic structure. The stainable substance is arranged in fairly uniform medium-sized granules, filling the cytoplasm, perhaps more uniform and larger than those of the afferent cerebral cells. The nucleus is large, frequently covered up somewhat, and more or less near the center of the cell; in other cells it stands in an area where the granules have disappeared and just form a peripheral ring around the cell; and again I have found it excentrically located, even bulging beyond the natural periphery of the cell, just as in the cells in which the neurite was cut; a condition which was found by Marinesco in locomotor ataxia, by Councilman and Barker in meningitis and by myself moreover in elderly people without any observed cerebellar or other affection. The dendrites are slender; the stainable substance in them is scanty and in granules rather than in short streaks. The description given here is that of transverse sections. In the oblique and longitudinal ones, the cells are strik-

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<sup>1</sup> *Le Cervelet, Etude anatomique, clinique et physiologique.* Paris, 1897.

ingly similar to the 'motor cells' of the ventral horns, except in shape and general arrangement. The cell-body is twice to three times as long as broad and the heavy terminal dendrites with the typical spindles take a longitudinal course. The lateral dendrites are not very numerous, but turn at once into a longitudinal course, frequently so that one branch grows caudad and the other cephalad. The neurite originates from the side of the cell-body. This observation explains many peculiarities of the cells shown on transverse sections. The difficulty of differentiating them from the 'motor type' may become of importance in the final criticism of the question: to what extent are the form and structure of a cell characteristic for its functional connections? We shall show in a future article to what extent the size of the cell and the architecture of the tissue generally are of importance for the arrangement of the Nissl-bodies. The connection between these cells and the fibers of the direct cerebellar tract are little known, perhaps on account of their oblique course; the upper course of the fibers is in the center of the restiform body and the termination in the cortex of the upper worm of the same and of the opposite side.

The cerebellar afferent neurones of the brachial region partly constitute the nuclei of Stilling (the homologue of Clarke's column in the cervical segments), partly unite into the external nucleus of Burdach; those of the cranial segments are much less localized (lateral nucleus, olives and red nuclei?).

The efferent cerebellar neurones are undoubtedly the Purkinje cells and the cells of the central nuclei of the cerebellum. While the course of their axones is a matter of varying opinion, the structure of the Purkinje cells is so well known that we outline it here for the purpose of establishing another type of neurones.

The remarkably graceful silhouettes obtained with the Golgi method are familiar. Nissl gives the following description of this type of structure (*Z. f. Psychiatrie*, Vol. 54, p. 69): 'A careful study of a Purkinje cell not only reveals a net-shaped type of a structure but moreover stripes. The stainable bodies, embedded in the net-work so as to form, as it were,

the nodes of the net, are more or less plainly arranged in rows. They run parallel with the surface of the nucleus and form circles around it, at least along its base and sides but not towards its apex-process. These rows of bodies turn towards the apex where the meshy structure of the perinuclear part of the cell disappears and gives way to a purely striped arrangement of the stainable particles. On the pole of the nucleus situated towards the apex there are frequently rather large stainable masses like nuclear caps. These shields or crescents or irregularly shaped masses of stainable substance are peculiarities of this cell-type. Little is to be said of the structure of the processes since they consist largely of non-stainable substance. The basal process can be followed a short distance only; the apex process however for a great length. Although devoid of plain marks it appears striped evidently on account of the peculiar structural make-up. It is exceedingly difficult to fix the nuclei of the Purkinje cells; they are strongly inclined to chromophily. It is not difficult to see how different they are from the nuclei of motor cells.'

So little is known of the cells of the olives, pons, red nucleus etc., that we dispense with their description. They hardly figure as neurones yet except in diagrams. The midbrain mechanisms, thalami and corpora striata are not much less problematic, although much light has been thrown on them by v. Monakow. The data of knowledge of these parts cannot be incorporated yet in simple diagrams of neurones known in their totality with the exception perhaps of the ganglion habenulæ and its 'Anteile', and the fornix-apparatus.

For a complete summary of the safe data of the anatomy of the nervous system, we should add an analysis of all the less known types of cell-bodies in the various accumulations of gray matter, and further a summary of the unfinished analysis of 'white matter.' The progress from the old carmine stain to the Weigert myelin-stain and to the Marchi stain has led to an increase of facilities for the study of fibers and their states of myelinization and degeneration. Indeed the study of this point has become so easy that it is almost child's play and it is sur-



prising how many writers are satisfied with these superficial findings of tracts, without attempting to look for corresponding cell-bodies to complete the neurones. The time when ascending and descending degenerations and the length of the tracts of degeneration would pass as a description fit for publication is by no means over and much splendid material is thus half-way wasted because it is not exhausted with better methods of preparation and study.

One would think that the frequent cases of compression of the spinal cord surviving from a week to several months would have been used for settling what the degeneration method can settle in the anatomy of the spinal segments. In the vast majority of the few studies published, neither the cells nor the cephalic 'tracts' have been decently studied. Lately the writer received two such specimens, without spinal ganglia and without oblongata and brain. My well-meaning friends evidently have no exact conception of the extent of neurones.

Well-established 'systems' might well be called foundlings; we know nothing of the mother-cells from which they come. Among these are: Gowers' tract, a system of neurones constituting afferent elements from the lumbar cord-segments to the cerebellum and the midbrain; the so-called anterolateral descending tracts, which may come from the cerebellum, or midbrain or from Deiter's nucleus; the septo-marginal and comma-tracts which most probably do not come wholly from the afferent neurones of the spinal ganglia. It would further be important to revise the work of Flechsig from the neurone point of view; especially his idea of 'systems' which, he says, are the same as will degenerate in locomotor ataxia. I am inclined to attribute much of the common superficiality to the way students are usually taught. The phrases commonly used are: such a tract degenerates upward or downward and therefore conducts upward or downward. This may be shorter, and more easily remembered than the following attitude of mind dictated by the neurone-theory: any destruction of nerve fibers leads to a rapid *decay of the part of the fiber cut off from its nucleus*, while the fiber stump remaining in connection with the cell will usually

be found preserved in the adult and practically normal at the autopsy, apart, perhaps, from the atrophy due to disuse and from the characteristic alteration of the cell-body, the transitory, so-called traumatic, reaction. Only in the young do we find atrophy and even degeneration of the cell and remaining stump. Descending degeneration is the term used for the decay of fibers, the cells of origin of which are located 'above' a lesion; ascending degeneration a term used for the decay of fibers the cells of which are located in segments 'behind' a lesion. Such a statement gives the facts and at the same time the problems, and can be grasped by every man who deserves to be called a medical student, if the proper illustrations and demonstrations are furnished.

We cannot leave this sketch of the best-known neurones without a short statement concerning the *changes* observed in them *in normal and pathological conditions*, and especially *the interrelation of the neurones and their ways of interaction*.

For the neurone-theory the life-history of the elements is of fundamental importance. The early stages of development are well-known. It seems certain that a cell which has a specific process and is thus characterized as a nerve-cell, has lost its power of reproduction. Karyokineses become rare after the fifth month of gestation and the claim has been made that at birth the entire stock of nerve-cells is present, later growth of the nervous system meaning merely a growth of existing elements. The question is treated by Donaldson (*Growth of the Brain*, p. 163-171). Schiller's count of the fibers of the third nerve in the young and adult cats and Kayser's counts of cells in the cervical cord of the human foetus, child and man, show a discrepancy. Schiller found the number of fibers remaining the same. Kayser found an increase of *developed* cells up to adult life. It is probable that the discrepancy is only apparent; because we do not know how many *undeveloped* cells Kayser started with. From the presence of centrosomes found in a few cells (Lewis, Lenhossék, Dehler, etc.) no conclusion should be drawn now; the occasional karyokinesis not only of neuroglia

but of nerve-cells, in the healing wounds of the nervous system (see Valenza, p. 32 and A. Tedeschi, *anat. experimenteller Beitrag zum Studium der Degeneration des Gewebes des Centralnervensystems*. Ziegler's Beitr. z. path. Anat. Vol. XXI, H. 1, 1897) is hardly more than an object of curiosity. The occurrence of more than one nucleus, not infrequent in the sympathetic nervous system, very rare elsewhere, is also an uncorroborated fact. (See further the latest summary of this question: *Sulla cariocinesi della cellule nervosi*. Ricerche del dott. Giuseppe Levi. Riv. di Pat. nerv. e ment., Marzo, 1898.

Hodge has published a little study of the appearance of human cells at various ages, only referring to the cell-body, and on ground of three individuals. A diminution of the relative size of the nucleus in old age seems to be the best established result. The strongest part of the life-history of the neurone lies undoubtedly in the facts which led His to establish the neurone-theory from the embryological point of view (see p. 121).

There are a vast number of observations on experimental and pathological alterations in various forms of nerve-cells in the literature of the last two years, the effects of inanition, intoxications, diseases, etc. After summarizing the available material, the writer finds that only a small number of leading features throw any light on the neurone-theory. The majority of studies deal merely with the changes in the cell-bodies in preparations with Golgi's and Nissl's stains, or their modifications.

The history of our knowledge of functional changes in nerve-cells due to stimulation, exercise and intoxications has been written a number of times in late years. The principal contributions begin with Hodge, Mann, Vas, Nissl, Schaffer, Pandi, Sarbó, Berkeley, etc. They have established processes of fatigue and recuperation, of toxic disorganization with termination in death or recuperation, of very much the same character as those known in other cells of the body. About the details there is much controversy.

I refer, for a summary of the literature, to the memoirs of Giambattista Valenza (*cambiamenti microscopici della cellule nervose nella loro attività funzionale e sotto l'azione di agenti stimolanti e destruttori*. Napoli, 1896) and the excellent reviews of the *Rivista di Patologia*, *Revue neurologique* and *Neurolog. Centralblatt*, and especially to the studies of Nissl and Lugaro. As a concise and easily accessible statement of most of the data, the two general reviews by van Gehuchten and by Marinesco, offered to the Congress of Moscow, deserve recommendation. I give here a short account of the set of experiments made by Goldscheider and Flatau, also reported at the Moscow Congress and accessible in abstract in the *Revue neurologique*, Vol. V, p. 525.

1. The injection of 'malonnitrile' ( $\text{CN-CH}_2\text{-CN}$ ) produces violent phenomena of intoxication which disappear after the administration of hyposulphite of sodium. In connection with the intoxication one finds the Nissl bodies in the ventral horn-cells in a process of deformation and disaggregation; they become smaller and lose their regular and symmetrical disposition. The non-stainable substance and the nucleus take an equally intense stain. Under the influence of the hyposulphite of sodium all these alterations disappear within three days. It is of interest that the functional symptoms of intoxication disappear very rapidly, more rapidly than the morphological alterations of the cells.

2. When an animal is overheated to a temperature of  $109-112^\circ \text{F.}$ , the cells increase in volume, become homogeneous, opaque, and take a light blue color. The Nissl bodies are destroyed; the dendrites are pale blue, oedematous and varicose. The changes begin to decrease at once after the experiment, and disappear completely in two or three days. The same alterations, but less marked, are observed with a temperature of  $106-7^\circ$ , if at least this elevation of temperature is kept up for at least three hours.

In this experiment too the function recovers before the restitution of the anatomical changes.

3. The toxin of tetanus produces very characteristic nu-



tritive changes in the motor cells of the anterior horns, especially swelling and pallor of the nuclear bodies; increase, breaking up and finally dissolution of the Nissl bodies, increase of volume of the entire cell. These alterations are the more pronounced the greater the concentration of the toxin. The injection of the anti-toxin or the use of weak concentrations of the poison still allows the cells to return to their normal state, the swelling of the cell disappears and the nucleus takes on angular shapes and returns to its normal volume.

4. The greater the concentration of the poison, the more rapid the evolution of these alterations, and also the more rapid the restitution. Weak concentrations however produce very slow alterations which may persist two or three weeks.

5. The complete restitution of the Nissl bodies is obtained more rapidly than that of the nuclear body.

6. Not all the cells react exactly alike; one often observes noticeable differences of intensity in neighboring cells. Similar differences in the degree of morphological changes are observed from one animal to the other (individual peculiarities).

7. There is no accurate relation between the intensity of the phenomena of intoxication and the degree of anatomical lesions of the cells. These can manifest a tendency to regeneration at a time when the symptoms of intoxication are on the increase and the reverse may be noted. The same disproportion between the anatomical and the physiological phenomena has been ascertained by the writers in the experiments on 'malonnitrile.' This fact must be taken into consideration in the appreciation of anatomo-pathological findings.

8. The intravenous injection of the antitoxin of tetanus exercises a manifest influence on the evolution of cellular alterations by retarding them; preventive injection hastens the onset of the phase of regeneration.

9. The action of the antitoxin on the cells is beyond doubt *indirect*. It consists in the neutralization of a quantity of toxin bound by the cell.

10. The morphological alterations of the cell are the ex-

pression of a chemical connection between the toxin and the cell body. [?]

11. The injection of strychnine produces changes analogous with those produced by the toxin of tetanus. The first alterations set in sometimes as early as in three minutes. If the animal survives the experiment one also sees that restitution of the function precedes that of the morphological structure.

12. The analogy of the action of tetanus and strychnine on the morphological structure of cells suggests that the anatomical alterations are of great importance for the exaggerations of that excitability of the cells which is found clinically in these forms of poisoning.

This is a fair instance of the present position of the question. Studies of the axones and their terminations are not available yet and therefore the picture of the *neurone* is incomplete.

To judge from what was said of the direct motor neurones (see p. 255, etc.) the great problem is now as follows: are there two fairly distinct mechanisms in a nerve element, a vegetative element supplying the possibilities for nutrition and growth, and a functional element (the fibrils?), the substratum of neural activity? Or we might perhaps ask more clearly: are there two elements, the functional and the nutritive, held together by the processes of metabolism and growth, and, morphologically, by the nucleus? The present methods give no satisfactory answer to this because the stainable substance is the chief element brought out; and because diffusion of the stain (deeper coloration of the non-stainable paths and the processes) is only a very indirect criterion of the real condition of the 'fibrils.' This may be the reason why the clinical and morphological phases are not quite parallel and this again might justify us in assuming as a great probability the existence of such a *division of mechanisms into vegetative and specific activity*. The promotion of these studies depends largely on the improvement of technique. If Bethe's new fiber-method can give a perfectly reliable demonstration of fibrils in the cells and all their processes, we may remove many objections of fundamental importance, as those made by Held. On the same evidence will depend

our knowledge of the *process of regeneration*. This has some practical importance. There are surgeons who maintain that they observe a healing *per primam* of sutured nerves and a rapid re-establishment of function absolutely inconceivable from the point of view of the neurone-theory and especially of the fiber theory. These 'observations' are in serious collision with the results of the most careful experiments.

Before we pass to the second problem, the interrelation of the cells among one another, an interesting contribution of *Achille Monti*<sup>1</sup> deserves our attention on account of its fundamental importance as a possible method in the future.

Embolisms were produced by injecting powdered carbon or lycopodium in the carotid of animals. In surviving animals, killed about five days later, the Golgi method brought out small foci of alterations in neuroglia and nerve cells. The most striking result is that the dendrites suffer first—become varicose and lose the gemmules; the cell-body also becomes deformed and last of all the axone is affected. We must, of course admit that the method is that of silhouettes; but it is sufficient to show that in a cell near a focus only the dendrite directed towards the focus, may degenerate and the others, with cell-body and axone, remain quite intact. It is easy to see what a vast series of important data can be obtained from such studies when the right methods are developed.

In this connection we may also mention an interesting phenomenon observed by *Meyer* in the case of facial paralysis quoted above. The auditory nerve, being also involved on account of the hemorrhagic process in the internal auditory canal, showed at its termination a remarkable increase of neuroglia cells. The terminations of the fibers had evidently suffered more rapidly than the fibers and this decay had called for the neuroglia reaction. Moreover it was evident that the cell-bodies of the central 'auditory nucleus' were affected slightly, although according to present theories, they were only in *func-*

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<sup>1</sup> Sulla anatomia patologica degli elementi nervosi nei processi da embolismo cerebrale. Boll. della società medico-chirurgica di Pavia, 1895.

*tional* connection with the degenerating auditory fibers, as they belong to the intersegmental or cerebral afferent type. *Goldscheider* and *Marinesco* had formulated the opinion that for the normal vitality of a nerve-cell the normal stimuli were necessary. They would perhaps refer the above finding to the abolition of the conduction of auditory stimuli. Another explanation might be offered, namely, that the same condition which called for neuroglia-proliferation was also the cause of the alterations in the contact cells, and in this way we might avoid too generalizing theories by remaining on morphological ground.

Coming to the question of the interrelation of the neurones we must mention the work of *Held* which would if substantiated draw a veil of denial over many of the statements given so far. I refer especially to *Held's* last contribution<sup>1</sup> which may well be regarded with some apprehension by certain ultraprogressive speculators.

To fully understand the bearing of his view, we must return to the sketches given of the transmission of nerve-impulses on plate XV. To *Nansen* and *Golgi* the cell-body and its protoplasmic processes appeared as a vegetative mechanism; the conduction of impulses is perfectly intelligible through the axone and its collaterals. In 1891, *van Gehuchten* claimed to have found in the mitral cells of the olfactory bulb a cell in which no other conduction was possible than that through the dendrite to the cell, and through the cell into the axone. (That the arrangement of the olfactory cells does not give an *absolute* proof of this view has been stated in the abstract of *Monti's* paper on page 124. Even here recurrent collaterals play a rôle). *Cajal* took up this statement and illustrating it in his sketch of the cortical mechanisms he established it under the name of the 'law of dynamic polarization.' *Charles-Amidée Pognat*<sup>2</sup> gives a short account of the latest phases of this the-

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<sup>1</sup> Beiträge zur Struktur der Nervenzellen und ihrer Fortsätze. Zweite Abhandlung, von Hans Held. Arch. f. Anat. u. Entwicklungsgeschichte. Anat. Abt. 1897, p. 204-294, and plates IX to XII.

<sup>2</sup> De l'importance fonctionnelle du corps cellulaire du neurone, par C.-A. Pognat, Revue Neurologique, Vol. 6, No. 6, 1898.



ory. In order to do justice to the occasional origin of an axone from a dendrite instead of from the cell-body, and also to the peculiarity of the segmental afferent neurone, Cajal has, in his new work<sup>1</sup> maintained three 'laws' established by him:

1. The law of economy of time. In the spinal ganglia the cells are attached to the fibers so as to form a T. The conductors are thereby placed into the very axis of the ganglion and in the direction of the shortest way between periphery and posterior root; and the current need not pass through the ex-centric cell.

2. The law of economy of matter. In the midbrain of fish, batrachians, reptiles, and birds, there are certain fusiform cells, the axone of which originates from a dendrite. In this way the axone spares the whole distance between the *cell-body* and the point of the dendrite from which it originates.

3. The law of economy of space. The body, i. e. the most voluminous part, of certain neurones is (occasionally) placed in regions poor in dendrites or final arborizations of axones, for instance Dogiel's cells of the internal granular layers of the cortex.

'On careful consideration of the physiological meaning of the cell-body, one comes to the conviction that it presents nothing but the convergence of the protoplasmic expansion towards the origin of the axone, enlarged by the presence of the nucleus.' He adds in a note: 'The cell-body is after all only a segment of the conductor.'

We need not comment on these exaggerations of 'legislative tendency,' but refer to what was said of the efforts of *van Gehuchten* towards making the segmental afferent neurones appear lawful (see p. 266).

*Berkley* has probably been most explicit concerning the mode of contact between cell-elements, in the Johns Hopkins Hospital Reports, Vol. VI, p. 89-93 and plate XV (the intracerebral nerve-fiber terminal-apparatus and modes of transmis-

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<sup>1</sup> S. Ramón y Cajal. El sistema nervioso del Hombre y de los Vertebrados, 1 fasc. Madrid, 1897.

sion of nervous impulses). His first claim is that the fine end-branches of fibers are endowed with a 'protective sheath of great tenuity not easily recognized by ordinary methods of staining, which the silver method does not show at all. It is therefore more than probable that it is only at the free bulbous termination of the nerve-filaments (shown by the silver method only) that we have naked protoplasms, and from this uncovered nervous substance the dynamic forces, generated in the corpora of the cells, are discharged, through contiguity, on to the protoplasmic substance of other cells.' This limits the functional contact to these end-bulbs. Berkley further *assumes* the presence of a protecting membrane around cell-bodies and dendrites. The fine stems of the gemmules of the dendrites pierce this membrane and only the tips of the gemmules show free dendritic protoplasm. 'The number of end-bulbs (one on each terminal branch) of the association and ascending fibers from the lower regions is not numerous, seldom exceeding six or eight, and the form is that of an arborization of the nerve twig; on the other hand the terminations from the collaterals of the psychic cells are much more numerous on the final branches and show the disposition of his Fig. 1. 'The interpretation of the objective existence of the terminal apparatus of the nerve-fiber can be made but in one way, namely, that the impression conveyed from external sources to central cells and from local cell to local cell, is not accomplished by a diffusion of the excitation through the whole cortex, or even at various points along the course of the finer branches of the axons, but at single points, perfectly definite in their distribution, and that these points are situated only at the extremities of the nerve fiber, in the form of an histologically exact formation—the bulbous ending of the nerve fiber—which in itself constitutes the sole and only means for the carrying over of the cellular force from axon to dendron, and from cell to cell, and is in entire conformity with the conception of *Waldeyer* of the entity of the neuron, each cell standing as an unit in the nervous formation, and only in continuity with others at definite points.'

After these statements we understand how broad a line of 'facts' *Held* attacks with his publications. The first attack goes against the interpretation of the structure of the cell. On sections of 1 micron, *Held* could not convince himself of the fibrillary character of axones or cell-plasma. He corroborated the view of *Bütschli*. He sees the 'fibrils' connected by cross-fibrils. A thin section through a honey-comb would produce just the same appearance. In the axone *Held* sees this axo-spongium (simulating the fibrils) and the neurosomes, small granules embedded in the axo-spongium and especially numerous in the end-plates of the axones. *Held* has observed in the trapezoid nucleus of the medulla that the axones entering it form a sort of end-plate as they approach the cells. In the cells he distinguished the cytospongium, the neurosomes and the Nissl-granules, and he finds it possible to distinguish the axo-spongium from the cytospongium by a difference of stain. In an animal one or two days old, or in the new-born, the axone-ends form a basket-like surface of contact with the cell-body separated from it merely by a homogeneous line probably of ectoplasm of the nerve-cell (or axone-plasm?). In the animal nine days old, this limiting line cannot be seen. In this and in the adult the basket branches of the axone are quite plainly distinguished from the cytoplasm by the number of neurosomes and the stain; but in many places it is impossible to deny a conrescence between some of them and the cytoplasm. In a third part of this study (*Arch. f. Anat. und Entw.* 1897, Supplement Band, p. 273-312, plates XII-XIV), *Held* establishes the same facts with a more delicate method, insists on the *Axencylinder-endfläche* being in contact largely with the dendrites, consisting of a real net, not of interlacing but anastomosing axone-terminations, even so that axones from several neurones should enter into the mesh-work. He corroborates *Bila Haller's* findings in principle at least, the claim of anastomoses of dendrites in the spinal cord of adult teleosts, and the findings of true meshes by *Ballowitz* in the electric organ of torpedo, but refuses *Apathy's* net work of nerve-fibrils in worms. Why? He also examines Golgi specimens of the adult with the same result and attributes the gene-

rally adopted views to the study of embryonic material. He stands firmly on the ground of His as far as the primary origin of neurones goes, but establishes concrescences in the adult.

Anyone who examines the excellent drawings of Held and the account of his technique must admit that his data cannot be refuted by the available literature. However improbable his results seem, they seem so largely because for years we have with all our efforts tried to get rid of old views, gained less on ground of minute observation on all kinds of material than on the one which did best justice to the new demands. This was the embryonic material concerning which Held says explicitly that anastomoses could not be observed yet.

Personally, I cannot change from one view to the other as if I never had any, and I feel rather sceptical toward certain claims of Held, but certainly not to much so to not consider it unwise to disregard his findings. They appeal to me because they are at last again studies of tissues and not merely studies of 'cell-individuals' disregarding everything in the section that does not fit into the customary plan. It will however be necessary to prove the same conditions by preparations gained with the 'fibril-methods' of the future, before we can call ourselves convinced.<sup>1</sup>

With this view we must close the data we have on hand for the neurone-theory. The fact that Wiedersheim once saw motion in the nerve-cells of *Leptodora hyalina* and that certain differences in the tissues of the retina and nervous system during rest and activity have been observed, is in altogether too problematic a state to be discussed here. The reader is referred to van Gehuchten, 2d edition, p. 218-222.

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<sup>1</sup> Since this was written (May, 1898), Nissl has repeatedly announced that the neurone-theory has died under the weight of Apathy's and Bethe's discoveries. We shall take occasion to analyze his reasons for the return to a diffuse network, which, after all, is merely a 'fibrillary' edition of Golgi's *réseau nerveux diffus*.



### The Utilization of the 'Neurone-Theory' for Neuro-pathology.

While these data of histology and of experimental pathology cannot help being of ultimate importance for the establishment of a more accurate neuropathology which would be useful for clinical purposes, a candid reader of the foregoing pages will recognize that not enough is really gained yet to entitle us to the proud statement that the neurone-theory has revolutionized neuropathology and solved its great problem, the correlation of physiological and histological data.

In treating of the relation between the neurone-theory and disease we must recognize that the mere speaking of neurones instead of the old 'fibers and cells' is a relatively insignificant change; a concession which old established clinical and anatomical neuropathology is making to the new nomenclature and stand-point of histogenesis. We cannot even say that the cell-theory was quite a stranger in neuropathology before 1887; at least as far as the study of nerve tissue as a tissue is concerned, or when we consider Gowers' view of the motor paths. On turning the pages of a modern text-book of pathology one might even suspect that merely a correction of details had been the result of the revolution.

This is evidently not the opinion of men like Andriezen, who favors us already with a 'complete' outline of the pathological anatomy of psychoses, or of Cajal and Duval and their followers, who unveil the silhouette pictures of sleep, hypnosis, hysteria, etc. One would think that we have it all in black cells now; yet, in the main, the new diagrams are merely new editions of the old ones. The medically important recent discoveries are the recognition of the nature of the spinal ganglia, and the description of the fillet as a cerebral afferent apparatus. In view of the position taken by Gowers in 1886 the 'two neurones of the voluntary motor apparatus' are hardly a new addition and even the fillet might be claimed as a preneuronic acquisition. The further changes are largely changes in names. The connection of the direct cerebellar tract with the cells of Clarke's columns is described by Gowers on page 121 of his

1886 edition, and the other tracts of degeneration in the cord received their cell-bodies and become 'neurones' whether the cells were known or not, simply because the neurone-theory demands it.

The progress lies to a great extent in the *new formulation of problems*. The novelty makes itself strongly felt when we apply it to customary clinical thought. A constant and most clinical exponent of the new standpoint, *Goldscheider*, says in Nothnagel's *Pathologie und Therapie*, Vol. X, p. 96: 'the attempt to trace the pathological anatomical phenomena of the nervous system to the neurones, seems at first sight to lead to a certain *conflict with regard to the customary division* in diseases of the brain, cord and peripheral nerves. For the neurones belong mostly at the same time to the spinal cord and the periphery or to the spinal cord and the brain. But we have instances of a common and universal participation of the nervous system in diseases which we classify, according to the principal localization or the clinical character, as brain, cord, or peripheral affections. This customary classification will not decrease the value of the reference to the neurone.'

This characterizes a mixture of progressive and conservative spirit justified in a work for physicians trained in the old views and gives a hint as to what might come. Leyden and Goldscheider cannot expect, even if they might feel inclined to be revolutionary, that the practitioner would enter without confusion into the new spirit, into a completely revised system of neuropathology. But need the time be far off when the *growing generation* might be shown the field in its new arrangement? With this question we enter upon the core of the modern problems in neurology and also upon the more restricted point to be discussed in this essay.

The great share of the progress of neuropathology lies unquestionably in the beautiful discoveries along the lines of 'localization.' As soon as the physicians learned how 'motor memories' of speech and of all voluntary movements, became flesh in the shape of 'centers,' all the current thought focused on the search for more 'centers.' Many of them had been sup-

plied before and many since the cerebral localization came to honor. Around these 'centers,' the data of neurological teachings were arranged.

Everything points unquestionably to a verdict that this must be in a way the ideal plan of progress, with Morgagni's motto: *ubi est morbus?* if at least it takes the advice of his further statement: *Nulla est alia pro certo noscendi via, nisi quam plurimas et morborum et dissectionum historias collectas habere et inter se comparare*—the only logical true method, with limitations, though, which we often disregard over the desire of drawing conclusions.

We see both the neurological sciences work in this direction, physiology and anatomy. The former reigned supreme till lately, and it has given neuropathology its method of reasoning. With the coarse anatomy of the nervous system and the knowledge of 'centers' furnished by physiology, the diagnoses of nervous diseases are made. Real histology then furnished the *cell* in which the functions of the centers were 'produced,' and the *fiber-paths* which 'conducted' the 'discharges,' the functional energy ready made and stored up in the centers and leaving there its traces. This is the current conception of most medical men of to-day.

The minute anatomy in the hands of a Meynert may have helped to strengthen this attitude; first, by making the finer anatomy of the nervous system appear as an abstruse subject, and second, by creating the idea of the 'projection-systems' which has arisen from the center concept and can be manipulated theoretically without any real histological knowledge. This may explain why physiologists have been and for the most part are, absolutely devoid of interest in pure nervous anatomy. The blade of a knife used in the operation was the most accurate instrument of precision used as far as 'anatomy' went, until v. Monakow began to work out some brains coming from Munk's laboratory, and Langley and Edingen a few of Goltz's brains. Schaefer's excellent anatomy of the brain in Quain might be held up against my statement as an anatomy written by a physiologist. It is indeed the best descriptive anatomy in

the English language ; but it is not written from a stand-point which would keep in view the whole field of neurology, genetic, comparative, physiological and pathological, because it is forced into the frame of an 'anatomy.' The work in physiology done by Schaefer has only the remotest contact with that anatomy. Horsley and Gotch, in their remarkable conjoint study come probably next to methods of precision in detailed anatomy with purely physiological methods.

What v. Gudden and his pupils had long foreseen and done, has become more fashionable since the introduction of Weigert's medullary stain and especially the popularization of Marchi's method. *There*, in the production and study of lesions with secondary degeneration, is the beginning of physiological anatomy. It is on ground of these methods that the plan of architecture of the nervous system given in the second chapter has its foundation. Further elements are furnished by comparative anatomy combined with the degeneration method, and by the method of embryology and study of later development in man and animals (methods of His and Flechsig). Side by side with this are, of course, the physiological observations. The fact that the neurone-theory grew partly out of this combination of neurological methods, and finds its natural home in them, is one of the reasons why the Golgi-method should not be praised as the backbone of modern neurology in the customary exclusive fashion. That neither the 'neurone-theory' nor the Golgi method can bring exclusive salvation in neurology, has been shown by the third member of the great trio of Swiss neuro-histologists, Prof. Kölliker in Würzburg, who felt himself justified in opposing the non-decussation of part of the optic fibers on purely histological ground.

The great progress achieved through the present revival of histological research consists in the intimate union between so many methods and stand-points. The scalpel-physiology gives way to embryological, developmental, comparative, experimental and pathological histology and physiology and instead of centers of the old types, *mechanisms* are being unveiled and the deductions are more closely physiological than 'psycho-



logical' or 'métaphysical.' The old 'center' is a sort of homunculus, a mysterious pigmy who acts his part as a little man would, accumulates images and energies and discharges them, sends them along the wires of fiber-paths to his superiors and inferiors who discharge again on others. Such action is decidedly more anthropomorphic-electrical than physiological.

The plan offered here is one of physiological mechanisms, leaving open the ultimate question what the 'discharge' and the life-process of the individual neurone really is, but searching patiently for details of the relations of neurones and of the parts of neurones to one another. It turns against the tiresome habit of riding every detail-discovery to death by trying to explain through it the whole unknown and is more seriously bent on a large plan which shall not come into conflict with any of the possibilities of detail. It takes its base in the oldest and best-known and best-knowable, the segmental nervous system, and proceeds to the superstructures, the cerebellum, midbrain, thalamus and cerebrum, on this basis. At the same time it remembers certain general concepts of biology as not altogether out of place where general methods of reasoning are in question.

The medical literature shows a great deal of the standpoint of Cartesian localization left; however modified and diluted, it is Cartesian in principle. Nobody would, of course, search the pineal gland for the spring of all action, the 'soul'; but this same soul is, though split up a little, seated in the centers. A truly biological spirit trained in comparative anatomy and physiology would hardly embrace this attitude except perhaps for the carelessness with which we always use old-fashioned ways of speaking. To these consistent or casual 'Cartesians' I would like to recall the famous statement of Spinoza which may lead the 'psychologically' inclined students towards a more modern biological concept: *Et enim quid corpus possit, nemo hucusque determinavit, hoc est, neminem hucusque experientia docuit, quid corpus ex solis legibus naturae, quatenus corporea tantum consideratur, possit agere, et quid non possit, nisi a mente determinetur.*

The neurologist finds as material for his studies the living being, be it an animal or a person. This living object offers three series of phenomena: (1) The morphological series, including all the facts of visible and tangible anatomy and histology; (2) the physiological series, furnishing the material for the specification of energies which become evident in the process of vital manifestation. These are the two objective series. A certain number of the physiological processes may moreover involve a third series of phenomena, subjective in character, but none the less objective in many manifestations, namely (3) the psychical series. An adequate digestion and correlation of all these three series of facts by the mental activity itself constitutes our neurological science. We have just seen how the older physiological school grouped its data and how it differs from the one represented by the modern anatomical-physiological school which the writer would favor. We take for the time being an objective point of view, leaving out the psychical because we lack sufficient experimental means now to closely outline the 'psychical' part of the nervous system. (For this latter problem, to use a probably justifiable simile from our plan of the brain, we should have been able to produce in a living being a state of pure automatism where all the actions, even complicated ones, could be elicited but without consciousness; and we should then be able to examine the brain for the cells which have been 'paralyzed' for this purpose in an isolated manner. This seems almost inconceivable with our present methods and means, and it will therefore be a utopian task to search in this way for the *purely* psychical 'Anteile,' or superstructures of the nervous system. It is easy to see from this simile that there are extreme difficulties in the way of demonstrating which neurone-complexes are *absolutely* essential for psychic happenings, and also, that it would be premature to speak of the 'psychic' neurones simply because we suspect that they are involved in conscious activity. To call the neurones of the pyramidal tract (the motor efferent cerebral neurones) 'voluntary' motor tracts, may not be far from the truth, but their action is not necessarily conscious (hysteria, epileptic

equivalents, etc.). If we admit that practically every sensory-motor reaction, even the most complicated one, can be unconscious-automatic, under certain conditions mentioned, we conclude that a further mechanism of differentiation and association must enter into activity to allow the quality 'psychical' to come in as an additional biological phenomenon. These may be arranged all over the cortex, after the type of the ground-bundles for the real segments of the neural tube, or more definitely, in part at least, as Flechsig suggests by his association-centers. This point can certainly not be called settled now. Flechsig's data do not with necessity point in the direction of his interpretation. It is to be hoped though, that, by exclusions, we shall learn with sufficient accuracy which cells belong to the 'psychical' mechanism before the above positive experiment can be looked for).

In an analysis of the anatomical and physiological data we must avail ourselves of the biology of the cell, but not forget in doing so the whole organism. We do well to bear this in mind when we speak of neural mechanisms. We do not use the word mechanism in the sense of mechanics, but work with biological factors.

A biological entity, animal or plant, would roughly speaking show us two sides of life, vegetative and reactive. The two cannot be separated absolutely; but we can speak of these two sides or aspects, both of the organisms as a whole and of the individual cells at each moment. This is best illustrated by the following criticism of the reflex-arc. In most text-books the reflex-arc is represented by the following elements: (1) The afferent neurone, and (2) the efferent neurone in connection with a muscle. It seems more true to biology and to our actual knowledge of the nervous system, though, to think of the following points in a reflex, illustrated in the description of the segments: Suppose that it is possible to irritate one isolated sensory nerve-element, although the interlacing of the terminations in the skin would almost preclude even this. Assuming then, that we can stimulate one afferent neurone independently by a prick of the sole, we find that this cell sends many collaterals to sev-

eral segments of the neural tube, and towards many types of cells. Among them are cells connected with *various* groups of muscles (various kinds of efferent neurones, see p. 135), and intermediate cells, segmental or supra-segmental (see p. 141, etc.). Each cell is in a definite state of nutrition and by this and its connections represents the sum-total of its previous life; it is, as it were, 'attuned to' a certain range of reaction, will react to certain stimuli only with a characteristic action, while other influences would leave it passive. Among the many cells which are reached by the afferent nerve only those will react which are 'attuned to' a definite impulse and give the adequate reaction. Under no circumstance is it possible to stimulate ONE *efferent* cell, but a reflex-arc consists always of (1) an afferent (at least one), and (2) many efferent neurones of one group of coordinated muscles and (3) the necessary number of intermediate cells. If a certain stimulus is complicated, the state of excitation of the afferent neurone may be of such a character as not to 'appeal' directly to the *segmental* efferent neurones; *cerebellar* and *cerebral* afferent neurones however may respond to that form, and the functional groups of cerebellar and cerebral efferent neurones respond to the excitation received in the only way in which they can respond, through specially 'attuned' *segmental* efferent neurones. If the reaction is complicated we might call it automatic, following the customary concepts without subscribing to the uncritically accepted dogma that whatever is 'automatic' must once, have been voluntary and therefore conscious. Or the stimulus may produce such a state of function in the *cerebral* afferent cells that 'psychical' elements are the only neurones which take it up or respond to it, and from this the state of activity may, or may not, spread on to definite groups of cerebral efferent neurones, reaching either the motor apparatus of expression in the case of simple thought and speech, or other groups of segmental efferent neurones (voluntary and vaso-motor action.) In this way indefinite numbers of selections can be obtained. And we repeat, that these unconscious or conscious reactions presuppose three types of conditions. (1) A special stimulation of afferent neurones,



segmental, or segmental plus suprasegmental; (2) a definite vegetative condition and definite functional connections of all the elements concerned; and (3) definite groups of efferent elements.

This consideration shows us that a reaction is not to be compared to a piece of meat put into one end of a sausage machine and coming out as a sausage at the other; nor is it best to compare the process with a current; it is more correct to say that a chain or *complex* of nerve-elements gets into a state of coordinated activity; one element after the other takes up the state of 'tension' and the cooperation of the *whole* chain represents the neural activity in any reaction. It is a wave of agitation or of action passing over very heterogeneous material, involving some elements but not others. Or if we take the simile of a current we must realize that each link has its state of action for itself, each cell perhaps in all its branches, and it does not get the action from another cell but merely the impulse. This seems perhaps a mere speculation. I do not hesitate to call it so; the ordinary reflex-diagram, however, is also speculation, evidently less 'hampered' by facts, although we see it so often that we acquiesce to it as a 'fact.'

This concept of interaction of nerve-elements and the formation of systematic acts, etc., is in full harmony with the concept of the neurone. It considers many kinds of neurones with many interrelations, each with its value as a cell and yet part of the whole organism, capable of entering into many chains of neural activity. Experimentally these chains can be followed as Horsley and Gotch have done for electric stimulation, or perhaps by poisoning certain definite mechanisms, etc. But only a combination of all neurological methods will help us to arrive at more clearness. In the mean time the above plan would seem to furnish a fair working hypothesis.

In *clinical* neuropathology, the chains of neural activity become accessible to observation in two ways: (1) The contraction of voluntary and involuntary muscles, (and perhaps also of other tissues, in the retina, etc.?) and (2) the subjective mental side of the process. We observe *objectively*, as it were,

the results of the action of *segmental* efferent neurones only; and *subjectively* perhaps only the action of psychical elements in the chain with their connections with the apparatus of speech, etc.? This seems fairly probable. We do not know 'how' we contract muscles although we may know what we 'do'; nor do we know how the segment feels; we only know 'how' the 'personal,' or psychical, part of the chain reacts to what is going on in the segment. From the knowledge of these two factors we build up the psychological concept of 'sensory-motor' mechanisms.

It would lead us too far, were we to analyze here the methods of reasoning of neuropathology. What has been said must be sufficient to show that the connection of clinical with anatomical neuropathology has many difficulties apart from the difficulty of direct observation. The interpretation of findings is, indeed, very difficult as soon as one leaves the beaten tracks of the clinical parade-types. In current localization the great questions are: peripheral, spinal, central or psychic for the quantitative motor disorders; cerebellar or 'sensory' for the ataxias; peripheral, spinal, central or psychic for the disorders of sensation. For the parade-forms of nervous diseases these general types of localization may be sufficient: but there remain enough cases which will not fit, and enough diseases which give rise to a flood of perhaps unnecessary literature, simply because the localization-spirit is poorly directed by the spirit of faulty general pathology. The inefficiency lies not in the desire for localization, but in the use of an exclusively *topographical* localization.

The localization furnished with experiments of irritation or destruction of parts of the nervous system—we called it the scalpel-method—is roughly topographical. Now it lies in the very nature of the plan of the nervous system given with the views developed above that coarse morphological topography must yield to, or at least accept, the assistance of functional localization. This, we have seen, drops the divisions of the nervous system into brain, medulla oblongata, spinal cord and peri-

pheral nervous system in favor of: segments plus supra-segmental apparatus.

We should have to write a book if we tried to discuss the arrangements of the facts available in the entire neuropathology on the ground of the concepts dictated by our discussion. We cannot give more than a rough outline here. The neurone-theory is only part of the whole concept. Recent investigations have been turning around problems relatively immaterial for the general point of view to be taken in neuropathology. Detail-problems have dulled the interest in larger ones. Many students are remarkably well informed on all the shades of the 'contact-theory,' but with the same effect which we all know to come when histologists work only with oil-immersions and forget to get a broad frame for the details with the use of low powers.

We have seen that we get our neurological knowledge from three clearly independent series of data. Our efforts go in the direction of melting them into one, i. e. into an objective conception of the nature and work of the nervous mechanisms. The naive realism of 'common sense' achieves this correlation very rapidly, usually in the sense of the center-theory. 'Wherever you can destroy it isolately, there must be its center, and in the center are the images etc.;' this is roughly expressed its motto.

I shall try to show how an uncritical use of this point of view combined with a purely anatomical one leads to habits of thought not altogether safe. Without entering on the polemics concerning localization, we can state that the 'motor region' alone (Bastian) or the motor area plus the parietal (Starr) form the principal part of the ordinary highest sensory motor mechanisms. The path usually given for a 'sensation' is the one represented in the plan of the brain as afferent cerebral. The segmental afferent neurone sends a branch to the nucleus of Goll or Burdach (the former in the case of a lumbar segment, the latter in the case of the cervical); the impulse is communicated there to elements of the fillet and from these to elements of the radiation of the nucleus ventralis thalami. If this is correct we

should think that a cut anywhere in this path and limited to this path should cause anaesthesia to any irritation. This we know to be established for two portions of the path only. First, the afferent segmental neurone as far as its entrance into the spinal cord; and second, less convincingly, in the fillet from its nucleus to the thalamus; higher up only when a large part of the thalamic radiation and the cortex belonging to it is involved. In the 'segmental region,' the spinal cord, etc., the matter is by no means clear. Brown-Séquard, in a criticism of the experiments of Mott (which spoke in favor of the anatomical path) gave up the well-known plan of the immediate decussation which tries to do justice to the symptom-complex of the Brown-Séquard paralysis. He states that not only hemi-section of the cord but also section of the *posterior roots* in the upper thoracic segments may produce a hyperaesthesia of the hind-leg of the same side and an anaesthesia of the opposite side. Further, if by a hemi-section of the cervical cord a contralateral anaesthesia is provoked, it can be reversed into hyperaesthesia by a second hemi-section in the thoracic cord, whereas the hyperaesthesia existing on the same side passes over into anaesthesia. The Brown-Séquard symptom-complex undoubtedly exists, but the anatomical explanations are hardly adequate. If we add further peculiar facts, such as the paralysis of a limb when all its 'sensory' roots are cut while the motor are intact (Sherrington), and all the scattered data on hyperaesthesia, on muscular, tactile and temperature senses, we should begin to feel that certain activities of the segments escape our attention and make no psychical impression *except by the final results*. The result of a sum *represents* items, but is *not a picture* of the summation, just as little as the figure 7 should be a composition of the figures 3 and 4 as an evidence for 3 plus 4 being 7, or just as little as we are conscious of which nerves and muscles are going to contract and relax when we catch a fly. We are radically wrong if we try to translate psychic phenomena uncritically into anatomical structures and believe that the plan of analysis and subdivision of psychic processes can be read piece by piece in the parts of the anatomical substratum. To return to the simile: who



would think that from an analysis of the number 121 into 1 hundred, 2 tens, and 1 unit, we could get any *direct* light on the process of getting the sum of 30 plus 46 plus 45? And is it not the same effort if we believe we must speak of temperature fibers, muscular sense fibers, tactile fibers?—why not of hyperaesthesia-fibers?—while we only know small differences among the cells of the afferent segmental types? Are we not forced rather to think of thermic, static etc., *arrangements*? Yet Bechterew claims that the broad fibers of the posterior roots serve to the muscular sense and the fine ones to the cutaneous sensibility. And since we already possess the term aesthesioneura (Minot and Baker) we shall soon speak of myoaesthesioneura and dermaesthesioneura! It will be the task of neurological research of the near future to go to the bottom of these segmental localizations with a full recognition of the danger of 'psychological' neurology and the possibility in mind that many or all the qualities of 'sensations' and reactions are *products* of the function of mechanisms and that the *elements* of the 'psychical' products are not necessarily fit to be identified with the elements of the mechanism.<sup>1</sup> This cannot, however, stop our eagerness for progress and we must admit that we are in perfect sympathy with the most eager localizer. Our hope for the progress and future of neuropathology rests on localization as a first step to the research on the *nature* of the lesion. We *must* associate certain symptoms with lesions of certain groups of neurones and we can do that without in the least becoming untrue to the above principles, and, if we look closely, this has at all times been the method of the more conservative. Comparing many kinds of clinical types with the sets of lesion found

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<sup>1</sup> In a discussion of biological monism some one objected by saying: On monistic ground psychology becomes simply a part of neurology. To any one who shares that fear I should recommend to sacrifice at once the desire for unity and to keep at least the three series of experiences apart: 1. The morphological-anatomical, 2. The ergetic physiological, and 3. The psychical. It would be a pity if a desire for monism would obscure the necessity of critically separating these three series in biology. I hope the readers will accept the term 'psychological neurology' as simply meaning the uncritical mixing up of facts of neurological and of the psychical series.

in them, could not help furnishing certain rules of localizations which are clearly established. The difference of opinion refers more to the interpretations than to the facts established. The interpretation is indeed the point requiring most caution and this becomes at once obvious when we realize that the function as we know it is the outcome of activity of a whole mechanism and that the defect of function is not to be identified with the function of the diseased element by itself but as part of the functional mechanism. *If you cut one leg of a tripod, it will fall and still you will not claim that the tripod stands on this leg only,* although its loss implies inability to stand.

We have already stated that clinical neuropathology has only two series of observations to build on; the subjective—the observations and feelings of the patient, and the objective which is altogether depending on the segmental efferent neurones for its expression. The following sketch of general diagnosis on ground of our working-hypothesis is not essentially different from the ordinary plan; it has its origin only in the desire to use methods which will promote the principle of research, at the same time doing justice to all the facts. For this purpose we take with us *a fundamental idea the segmental plan of the body and the existence of supra-segmental mechanisms.*

We usually start with the study of the subjective series of data by ascertaining the general mental condition and reliability the general sensation, the function of the special senses and the common sensibility, because these are necessary data and because during their systematic examination many points concerning the second series, the motor phenomena, will attract our attention. We proceed as is commonly outlined in the textbooks, searching methodically for areas with any of the known qualities of sensory disorders. The results must be so arranged that we readily connect them with a localization of the possible lesion, using the distribution and qualities of a disorder for a guide.

We begin with the sensory examination of the olfactory segment, and proceed to the optic segment, which illustrates best the general method. We need a knowledge of the gen-

eral visual power, and of the field of vision of forms and colors. If there is a defect we exclude first mechanical disorders (of refraction etc.), then affections of the retina and optic nerve; then we examine the reflex-irritability; if a scotoma was discovered, especially for the area of the scotoma. This is of special importance for the discrimination of certain forms of hemianopsia. Finally we search for subjective optic phenomena (from the phosphemata to real hallucinations). Clinical and anatomical pathology have furnished tables for localization and we distinguish the symptom complexes of:

1. Mechanical lesions (optic disorders).
2. Lesions of the retina.
3. Lesions of the afferent optic neurones.
4. Lesions of the cerebral afferent neurones.
5. Lesions of intracortical or general character.—We

need not speak here of group 1 and 2. For group 5 are characteristic: concentric constriction of field of vision and reversion of the color-fields, and the more complex subjective phenomena (hallucinations, fortification lines etc.). Lesions of group 3 and 4 are distinguished largely on anatomical grounds (presence or absence and kind of hemianopsia), the involvement of the 'reflex-arc,' the appearance of the disks and especially accompanying lesions of other mechanisms, as hemianaesthesia, hemiplegia, mimic paralysis, etc. We must make here the reservations necessary on account of the peculiar course of the reflex path which is still under discussion (Redlich, Bechterew, Massaut).

Next would come hearing (mechanical, segmental afferent or cerebral afferent lesions, or psychic condition?), taste (lesion limited to the segment of the 5th, 7th or 9th?) and finally the general sensibility. It would go altogether beyond the domain of this essay to detail all these points. I have done as much as I did in order to illustrate the method of correlation of data of clinical and anatomical pathology, and merely add, that for a diagnosis of 'sensory' lesions we must know the domain of the branches of peripheral nerves, of the plexus, of the nerve-roots and spinal and cranial segments, the hemian-

aesthesias with or without hysterical stigmata, or stereognostic disorders, etc.

In the objective motor sphere we look out for affections of the muscles and groups of muscles in reflex and complex activities (referring them in a similar manner as in the sensory sphere to special nerves, plexus, or segments, according to their distribution) and the character of the disorders present. If we find any disorder anywhere, we have to examine first for those symptoms which are associated with lesions of the segmental efferent neurones (the *direct* motor neurones of Goldscheider). This is necessary, because *motor symptoms produced by any disorder of a mechanism will only come out clearly, if the links between it and the muscle are in a normal condition.* It is therefore of great importance that we know very valuable tests for the condition of the segmental efferent (direct motor) neurones. The cardinal points (flaccid paralysis with atrophy of the muscles, absence of reflexes and electrical reaction of degeneration) are to be excluded in every instance before a disorder is looked for beyond. With a lesion of the indirect motor neurones (the cerebral efferent or voluntary motor apparatus) we associate an involvement of certain groups of muscles coordinated for special movements and joints, a tendency to rigidity, usually no atrophy, exaggerated reflexes and clonus, but normal electrical reaction, i. e. none of the symptoms associated with lesions of the direct or segmental motor neurones. Another group of symptoms is characteristic for mechanisms of a more specialized, perhaps psychical character, commonly called the group of psychic motor disorders, usually involving the entire limb (for instance both legs) or only special uses of the limbs (astasia-abasia, etc.).

A further type of motor disorders which requires investigation is formed by the ataxias, associated either with lesions of the motor cortex and the afferent cerebral neurones, the fillet (motor ataxia), with tumors of the frontal lobe (?), with lesions of the cerebellar apparatus and also with affections of the afferent segmental neurones (tabes and pseudo-tabes), forms which experience teaches us to distinguish; the motor ataxia existing



only on motion as awkwardness, the cerebellar showing more over the typical dizziness, the tabetic ataxia characterized especially by abolition of the reflexes in the parts affected and by defects of sensibility, and the pseudo-tabes by a different clinical picture, and especially combination of sensory defects with motor disorders of the 'peripheral' type.

General pathology of the nervous system teaches us to distinguish focal lesions and diffuse affections. My own point of view would lead me to insert affections of special mechanisms (writers' cramp and other localized disorders of limited, and therefore localized, mechanisms). For the usual purposes we can get along with the two classes mentioned. The general advice is, that a symptom-complex which can be explained by a lesion of one point in the nervous system, should be referred to it; symptom-complexes explicable by two focal lesions only are to be taken with caution, and if numerous lesions would be necessary for the explanation of the symptoms, we do best to think of the possibility of general disorders (toxic, infections or asthenic). Where no evidence is present of a segmental affection but a whole side or the face or arm or leg alone show the symptom-complex of the cerebral-efferent system, we are almost certainly dealing with a lesion in the supra-segmental region, the motor region or the internal capsule. A concomitant disorder of the stereognostic sensibility would speak in favor of the cortical seat of the lesion; a purely motor hemiplegia for an affection of the internal capsule, etc. In other words, the condition of the movements and the muscles prove the existence of a lesion of the cerebral efferent system; but the question 'where is the lesion located *within* this system' must be settled by concomitant symptoms. Thus, we make our diagnosis of the rare hemiplegia alternans on the ground of the symptom-complex hemiplegia plus segmental affection of the third or seventh nerve, as the case may be.

Or we find a spastic paralysis of both legs. It may be due to a transverse lesion, in which case we get also certain segmental symptoms, or it may be pure 'lateral sclerosis' as

far as our symptomatological diagnosis goes, if we miss completely the segmental symptoms.

All this shows an important rule on which H. Jackson insists strongly, namely that it is impossible to say from the *character* of the symptoms, in which place of one neurone or system of neurones the lesion is located. The symptoms give evidence that the neurone is deranged in its function; whether in the dendrites or the cell-body, or the fiber or the final arborization, cannot be said from the symptom but merely from association with other symptoms referable to other neurones or mechanisms. Returning to the instance of the lateral sclerosis, we would say that the absence of all symptoms which would refer to some other neural system, limits us to the disease of the cerebral efferent system and the limitation of the symptoms to the legs makes us expect that only the pyramidal system below the brachial segments is affected. If the process were one-sided and involving the arm, it might be impossible to differentiate a simple degeneration of fibers from the effects of a slowly growing tumor. The writer has lately seen a patient in whom the assumption of such a tumor becomes more and more improbable on account of the long duration (six years), slow development of the hemiparesis and beginning affection of the opposite side. Here it is empiricism that decides; not the symptom of the neurone-complex.

This leads us over to the diffuse diseases which may be called diseases of certain levels, following H. Jackson's nomenclature. There are certain etiological and pathological entities which are limited in a peculiar manner to certain types of neurones. Not all the cells of one type are affected (just as in the experiments), nor are all the segments of the body equally apt to be involved. Thus, to pick out a classical instance, locomotor ataxia consists of a lesion largely of the intra-axial (central) branches of the segmental afferent neurones, those elements which are drawn in blue in our chart. Other cell-types, except perhaps the intersegmental association-elements of the posterior horns, are not regularly and systematically enough involved to command attention clinically. Now we know that this most

probably metasyphilitic affection may begin with the optic nerve and stay there, or may begin in the leg segments (shooting pains, etc.) or rarely on the ulnar side of the arms, and only very rarely on the pneumogastric (gastric crises). Edinger attempts to explain this by differences of resistive power in the various segments on the ground of his 'Ersatz-theorie' (see his article in Volkmann's Vorträge).

The following is a summary of the diseases in question, closely following the outline given by me in an article published in 'Medicine,' May, 1896.

I. Poisons which cause *segmental* affections with almost exclusive involvement of the motor side.

1. Acute anterior poliomyelitis, or acute infantile paralysis: degeneration of the anterior-horn cells, motor fibers and muscles for one extremity, rarely for two, practically never involving the afferent side, and hardly affecting the supra segmental apparatus. (Strümpell's acute encephalitis is, to judge from the analysis by Oppenheim, hardly proven to belong to the primary affections of nervous elements, but would require further study from this point of view).

2. Lead poisoning: affecting largely the motor elements belonging to the musculo-spiral nerve, more rarely those of the ulnar and median nerve; in rare cases only the supinators and biceps, brachialis internus, and deltoid are involved (Remak's type). It rarely affects the peroneal nerves. In very severe intoxication, the paralysis may become generalized, and especially in these cases involvement of supra-segmental parts—encephalopathia saturnina—is marked, the minute anatomy of which is not clearly known, and the accurate study of which is difficult on account of the existing disorder of the 'lowest level,' i. e. the segmental motor neurones.

3. Apparently we should be forced to put down here the cases of Landry's paralysis. The usual types have been found to be largely polyneuritis; many of them also showed sensory disturbances and reaction of degeneration of the muscles. Thus an analysis of the cases leads one to the conclusion that Landry's paralysis is a symptom-complex occasionally met with

in acute nerve intoxication, perhaps merely a phase, usually transitory, rarely persistent throughout the disease.

4. Post-diphtheritic paralysis, involving most frequently the muscles of the palate, of the eye (m. ciliaris, rarely abducens), of the pharynx and larynx. Much more frequently the knee jerk is lost. Later paraesthesia may set in, and a diffuse paresis with hypoaesthesia, especially also with incoordination, and the so-called diphtheritic pseudo tabes develops. This secondary symptom-complex forms indeed the most remarkable 'peripheral' instance of a transitory, usually curable, counterpart of the locomotor ataxia of metasyphilitic origin.

II. Segmental affections with both motor and sensory disturbance:

1. Certain occupation pareses.

2. The typical infections or toxic or asthenic polyneuritis: paraesthesia and anaesthesia of the extremities and paralysis usually beginning with the extensors. The most prominent forms are:

Alcoholic neuritis with great tendency to involve the cerebral mechanisms—deliria and typical 'polyneuritic' psychoses being most frequent in this form.

Arsenical neuritis—acro-neuritis. In a case of Henschen's there was also plain affection of the 'spinal cord' with a (secondary?) hemorrhage. In a case lately observed, the cranial nerves became involved and delirium set in (involvement of the highest mechanisms?).

'Polyneuritis' following other infectious diseases—tuberculosis, malaria, influenza, typhoid, etc.

Endemic forms: beri-beri.

Anemia and cachexia (auto-intoxication?), diabetes, senility, etc., produce similar clinical symptom-complexes.

Finally a certain number of cases in which the etiology is difficult to ascertain, including especially many cases of Landry's type, etc.

III. Segmental affections, chiefly sensory. The prototype of this group is one form of the metasyphilitic nerve-intoxication, locomotor ataxia, affecting largely the intra-spinal



and intra-cerebral processes of the segmental afferent elements, and in rare cases the segmental motor elements, in still rarer cases also the pyramidal tracts ('combined sclerosis'), and finally going over into the preeminently-cerebral type, general paralysis.

IV. Unknown influence causing a chronic degeneration of the terminations of the cerebral efferent motor system—lateral sclerosis, sometimes involving also the segmental motor system: amyotrophic lateral sclerosis. In H. Jackson's nomenclature, this group would form the 'middle-level' lesions, occasionally involving also the lowest level elements, my 'segmental' neurones.

V. Finally, the alienist may be allowed to add as highest-level forms of acute intoxication or exhaustion those 'mental diseases' which Kraepelin classifies as delirium of intoxication or exhaustion, and also those cases of general paralysis which run too rapid a course to have marked symptoms from the cerebral efferent and segmental mechanisms—'typhomania or delirium grave.'<sup>1</sup> They are processes preeminently involving the intracortical mechanisms.

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<sup>1</sup> The pathological anatomy of all these diseases seems somewhat unsatisfactory for those who expect merely lesions of 'neurones.' In end-stages the lesions of the neurones may form the most striking part—as the absence of large cells in the residuals from anterior poliomyelitis. But the acute process is a disease of the *tissue*, as the drawings of Goldscheider will show (Nothnagel's *Spezielle Pathologie und Therapie*, Vol. X, pp. 418-422, figs. 20, 21a, 21b and 22). Saying that a boy has an anterior poliomyelitis should indeed be distinguished from 'he has residuals from an anterior poliomyelitis.'

The *diagnosis* must for these reasons always contain two factors: 1. *The pathological entity*—the disease-process as such with the etiological side—for instance nerve-degeneration on ground of chronic alcoholic intoxication; or for poliomyelitis: acute or chronic poliomyelitis (infectious—with fever—or toxic? etc.).

2. *The diagnosis of the scope*: affections of which segments, total or partial, coincident with the districts of which 'peripheral nerves,' plexus roots or spinal segments, involving which supra-segmental apparatus, etc.

That such a diagnosis becomes a little lengthy, need not alarm us. It contains the decision of the essential questions which arise when we proceed to the prognosis and formulation of treatment.

From all that was said from the clinical point of view we need charts of the sensory surfaces of man giving :

1. The districts of distribution of the nerves after they emerge from the plexus, i. e. the really peripheral branches.
2. The distribution of parts of the plexus.
3. The distribution of the posterior roots.
4. The distribution from the cross-lesions.
5. The distribution from lesions of the fillet, and the known clinical types of cortical foci.
6. Types of distribution in hysteria.

It is evident that the data for all these charts are partly widely scattered, and partly not available yet. But the work of the last years has filled many gaps and if more people knew where the gaps are, more would keep their eyes open.

On the side of motor observations we should return to Duchenne de Boulogne. Muscles and muscle-groups should be presented in the charts.

1. The muscles depending on definite peripheral nerves.
2. The muscles depending on parts of the plexus.
3. The muscles fed by each anterior root (segmental distribution).
4. Types of involvement of the cerebral efferent tract (pyramids), and of cortical 'areas.'
5. Types of segmental and supra-segmental lesions—cross-lesions of the tube.

These charts must naturally be the result of many clean observations. They will become the expression of definite clinical data comparable with anatomical data in a dissection of the anatomical substrata, after the plan given in the charts of the general and minute architecture.

To sum up: Let us remember once forever that the phrase 'Ubi est morbus' does not mean 'which symptom to which neurone.' We have, for our diagnostic reasoning, three really independent series of facts, each series complete in itself; a motor (objective) series, a sensory (subjective) series and an anatomical series of data. We have to blend these together to get the picture of the disease. The motor series, and the sen-

sory series are both as it were 'functions' of the anatomical series. The motor series expresses the effects of the action of all the anatomical mechanisms in the form of contraction of muscles; the sensory series the effects of the same action of all the mechanisms in the form of activity of the psychical apparatus. Only the direct (segmental) motor neurones have their action expressed directly; even the psychical apparatus manifests its activity merely by the motor neurones (voluntary and sympathetic), and all the mechanisms are known to us merely by their effects on these. Parts of these results cannot be compared directly with parts of the mechanism if we do not care to stand in the way of our own progress as in the vexed question of the localization of 'sensations' in the segments of the neural stem.

#### Retrospective Considerations.

The neurone-theory has for us the value of a working hypothesis. It is closely connected with the cell-theory of tissues generally. Many detail features, as the question of anastomoses, although they may be essential for the formulation of certain versions of the neurone-theory, are still problematic. The genetic side of the neurone-theory, the exclusive origin of all the portions as parts of cells—is endorsed by almost everybody; the persistence of all these portions,—fibers, fibrils, etc.—as parts of cells is also maintained by the great majority for the nerve-elements but is abandoned by Weigert for the neuroglia. The importance of Nissl's, Bethe's, Apáthy's and others' objections is not sufficiently cleared yet. The independence of the nerve-elements in the foetus and in the young is also generally admitted; but the question of ultimate anastomoses in adults is just now more unsettled than ever before.

The laws of degeneration give a valuable line of support to the cell-theory. The trophic influence of the cells on the fibers is now reduced to the general laws of trophism of cells, especially since we know that the relations of trophism between fiber and cell are quite mutual, the cell-body being affected by lesions of the fiber just as well as the fiber by a break of its

connection with the cell. To what extent the visible changes of the cells during fatigue and intoxication are accompanied by changes in the fibers, is not accessible yet to our methods; this is a problem for the future; and for this reason it seems impossible just now to decide from histological findings whether the specific energy, whatever it may be, is produced in the cell-body or whether the cell-body merely furnishes the nutritive material. As to the detail structure, the nucleus is not specific for nerve-cells, although, of course, each type of cells has a characteristic form of nucleus. The Nissl-bodies are commonly recognized as containing masses of nutritive material, preformed or merely precipitated in the sections in the meshes of the non-stainable substance. The latter is the subject of ardent controversy. Held defends the Bütschli-theory of the spongy (wabige) structure of protoplasm and looks upon the fibrils as the optic representation of the walls of a series of meshes or of a honey-comb. The majority favor, however, the Filartheorie, or fibril-theory. On the interpretation of the findings of Held by Bethe's unpublished fibril method or some equivalent, a great part of the points of contest will depend. Not till then shall we be able to say whether the fibril or the neurone is the unit of the substratum of nervous activity.

In the meantime it seemed most practicable to ascribe to the neurone (the genetic cell-unit) a function as a unit.

Whatever the function may be, we do not contradict any established facts by assuming that the cells of the same type and structure will probably have a similar range of connections. The variety of functional activity is thus ascribed: 1. to varieties of cell-type; 2. to the fact that the cells are connected among one another in various ways so as to form various mechanisms. What we know clinically as function (i. e. as equivalents of motion and chemism) is always the expression of the activity of a whole *mechanism* and we are not conscious of the activity of the individual neurone except through the results of its action in a *chain*. Further, what we know from electrical tests cannot be identified directly with the action; it is at best



an *index* of action, since it is seen in non-nervous tissues also (the muscles).

The physiologically simplest and best known neurones are the segmental motor ones. On their integrity depends the *objective* demonstration of all disorders of other neurones. The afferent neurones can be analyzed indirectly only, as far as their individual function goes. It is not improbable that the specific function of the afferent neurones depends on the segmental and suprasegmental *connections* of the mechanisms.

Considerations based on comparative neurology and on the results of experimental anatomy recommend the adoption of a plan of the nervous system which favors the study of functional mechanisms. Instead of starting from the most differentiated, most complex and anatomically least known cerebral centers, we take the segmental motor neurones as a basis, those neurones which grow in the basal lamina of the neural tube (or neural stem) on either side of the raphe, and connect through their axone with definite muscle-fibers, blending with them to a functional and even trophic unit. We divide them into segments according to the 'peripheral nerve-roots' and their function. Afferent neurones from the spinal and cranial ganglia combine with them to form segmental mechanisms with the help of intermediate (association or rather dissociation) cells. Differentiation of function is obtained by the growth of specially connected mechanisms, probably working so, that the (first) cells of the mechanism 'learn' to react mostly to the stimuli serviceable to the function of the whole organism. The simile was used that the cell is 'attuned' to special stimuli only. Apart from the segmental and intersegmental mechanisms, we have found suprasegmental mechanisms, anatomically lifted out of the neural stem as cerebellum, midbrain-ganglia and thalamo-cerebrum. On ground of the experimental data we recognize in them 1. the *body* of the special organ, 2. the afferent neurones ('intermediate neurones' of the segments sending their processes into the special organ) and 3. efferent neurones (cells of the special organ sending their fibers into the segments or into the other suprasegmental mechanisms). The advantage of

this method lies in the clearness of its problems and in the parallelism of its problems with those of the tasks of pathological anatomy and of physiology. And just here the neurone-theory in its broad and loose form is the most stimulating and workable hypothesis.

The method of correllation of clinical observation and the data of pathological anatomy has been discussed fully. For the physician who is satisfied with a hasty diagnosis the warning laid down may be superfluous. To him it does not matter whether the sun turns round the earth or the earth round the sun, as long as night is night and day is day and each comes in due time; but for the science of neurology it is essential that correlations shall be made critically. We have already summarized this point at the end of the preceding chapter.

## DESCRIPTION OF FIGURES.

### PLATE XX.

*Fig. 7.* Sections of hemiplegia with degeneration of the direct and crossed pyramidal tract.

A. Cervical cord in infantile hemiplegia. Complete resorption of degenerated direct bundle and shrinkage of the whole side of the crossed tract.

B. Cervical cord in hemiplegia of the adult. Greater stability of form and greater neuroglia scar.

### PLATE XXI.

*Fig. 8.* Section from a guinea pig in which the left hypoglossal nerve had been torn out shortly after birth. From Forel's contribution to Kölliker's Festschrift, 1891.

*l. p. m.*, left pneumogastric motor intact; *r. p. m.*, right pneumogastric motor intact; *l. hy.*, left hypoglossal nucleus degenerated; *r. hy.*, right hypoglossal nucleus and nerve intact; *rp.* raphe; *IV*, beginning of fourth ventricle.

*Fig. 9.* Section from a guinea pig in which the right pneumogastric nerve had been torn out shortly after birth. From Forel's contribution to Kölliker's Festschrift, 1891.

*l. s. X.*, left sensory nucleus of n. X, terminal branches of n. X intact; *r. s. X.*, right sensory nucleus of n. X, cells crowded, terminations of n. X resorbed; *l. m. X.*, left motor nucleus of n. X, intact; *r. m. X.*, right motor nucleus of n. X, degenerated; *l. hy.*, left hypoglossal cells and nerve intact; *r. hy.*, right hypoglossal cells and nerve intact; *IV*, beginning of fourth ventricle.

# OBSERVATIONS ON THE WEIGHT AND LENGTH OF THE CENTRAL NERVOUS SYSTEM AND OF THE LEGS, IN BULL-FROGS OF DIFFERENT SIZES.

By HENRY H. DONALDSON.

## CONTENTS AND SUMMARY.

### Introduction.

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- IV. Influence of water absorbed by the living frog on the weight of the brain and the spinal cord.
- V. Chart showing the weight and length of the brain and spinal cord.
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- VIII. Explanation of entries in Table 7.
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- X. Growth.
- XI. Chart II showing growth changes in the brain and spinal cord.
- XII. Explanation of Chart.
- XIII. Observations on the legs.
- XIV. Weight of leg muscles.
- XV. Length of leg bones.

## SUMMARY.

(1). In the Bull-frog the relative weight of the brain compared to that of the spinal cord decreases as the frog increases in size. The relative weight of the brain is temporarily increased in frogs kept dry for twenty-four hours before death.

(2). The weight of the leg muscles compared with the weight of the entire frog, slightly decreases as the frog increases in size. In frogs of all sizes, the muscles of the

thigh weigh 1.8 times as much as those of the rest of the leg.

(3). In frogs of all sizes, the sum of the lengths of the leg bones is a nearly constant fraction of the length of the entire frog. The proportional lengths of the several bones are also nearly constant.

#### INTRODUCTION.

In order to carry out another investigation on the innervation of the leg of the frog, it became necessary to determine the relations summarized in the title of this paper.

Of all our frogs, the Bull-frog (*R. catesbiana*) exhibits the greatest variation in size. It was therefore chosen for study in this case and all the statements given below are to be restricted to this species until their applicability to other species has been shown. The results in their first form are exhibited in Table 7 and Chart 1. Accompanying the table are to be found all remarks concerning the methods employed and the conditions observed during the investigation and the reader is referred to that part of the paper for such data.

We may therefore at once pass to a presentation of the evidence from which the conclusions stated above have been drawn.

#### I. THE WEIGHT OF THE BRAIN AND SPINAL CORD.

The proportional weight of the brain and spinal cord decreases as the body-weight of the frog increases. This is shown in the following table:

Body weight in grams.	Weight value of Brain.	Weight value of Spinal Cord.
1.32	1.89%	.68%
3.53	1.19	.45
37.46	.34	.14
199.10	.10	.05
313.50	.06	.03

In this, Table I, as in the other subsidiary Tables, which follow, the cases are taken from Table 7, and the calculations are based on the numbers there given. Each case can be identified in Table 7 by the body weight, as given above.

In this investigation, no difference in the weight of the



central system according to sex has been observed, but it would require a large number of observations on frogs of the *same* body-weight to properly demonstrate any difference of this sort. The records therefore have not been separated according to sex.

Table 1 also shows that the proportional weight of the brain decreases more rapidly than that of the spinal cord. This is again shown, in a slightly different way, in Table 2, in which the smallest and largest frogs of the series are compared directly.

TABLE 2.

Body weight in grams.	Weight of Brain in grams.	Weight of Spinal Cord in grams.
1.32	.025	.009
313.50	.215	.106

On comparing the brain weights in Table 2, there is found (by dividing the larger by the smaller) an increase of over eight fold, whereas the spinal cord has increased nearly twelve fold, thus confirming the statement concerning the more rapid enlargement of the cord.

The foregoing figures are based on single observations and hence are liable to vary as the individual observations vary, but the individual variability is so small that this general relation is affected by it to only a trifling extent.

From the difference in the rate of enlargement, it follows that the ratio of the weight of the Brain to that of the Spinal Cord normally decreases as we pass from small, to large frogs.

Using the same observations as were employed in Table 1, and recording only the number of times that the brain exceeds the spinal cord in weight, we obtain the following:

TABLE 3.

Body Weight in Grams.	Ratio of Brain Weight to that of Spinal Cord.
1.32	2.77
3.53	2.62
37.46	2.36
199.10	2.02
313.50	2.02

This change in the relative weight of the brain has been found in all vertebrates in which the relation has been studied.

For comparison we may take the observations on man and the white rat. In man between birth and maturity, the spinal cord increases about twice as fast as the brain. In the white rat about three times as fast, while in the frog, as shown above, the increase is only one and three tenths as fast. Thus it appears that in the frog the weight relations of the brain and spinal cord undergo less change during later growth, than in either the white rat or man.

## II. RATIO OF THE WEIGHT OF THE BRAIN TO THAT OF THE SPINAL CORD.

In the Table 3, just given, this ratio shows a steady decrease, the individual observations being widely separated from one another. If, however, consecutive observations are taken, the variability in this ratio becomes evident.

From the frog weighing 27.33 grms., to the one weighing 233.79 grms., inclusive, there are in Table 7, twenty-one complete records. These records, taken in the order of the body weight, have been divided into three groups of seven each, and the groups are here designated as A, B, and C. In Table 4, are given the ratios for each case in each group and at the foot of the column, the average for the entire seven cases forming the group.

TABLE 4.

Showing ratio of brain weight to the weight of the spinal cord.

Group	A	B	C
	2.55	2.22	2.23
	2.46	2.46	1.96
	2.23	2.01	2.21
	2.32	2.41	2.02
	2.36	1.98	2.09
	2.35	2.07	2.21
	2.31	2.19	2.25
Average	2.37	2.19	2.14

Here again the average ratio is seen to decrease as the frogs forming a given group increase in weight. To discuss, however, the variations in the ratio occurring between consecutive cases, it will be necessary first to state some of the conditions influencing the weight of the central nervous system.

### III. POST-MORTEM CHANGES IN THE WEIGHT OF THE CENTRAL NERVOUS SYSTEM.

During the first twenty-four hours after death the central nervous system of a frog killed by ether or chloroform exhibits a remarkable power of absorbing water from the surrounding tissues.

During the month of August the frogs, which are given in Table 5, were weighed, then killed and the legs removed and examined at once. The remainder of the frog was kept cold in a refrigerator for twenty-four hours and at the end of that time the brain and spinal cord were removed and weighed. The results are here given :

TABLE 5.

*After Twenty-Four Hours.*

Fresh Body-weight in grams.		Weight of Brain in grams.	Weight of Spinal Cord in grams.
	265	.303	.150
	271	.302	.141
	293	.303	.149
Average	276	.303	.146
No. 51C.	272	.202	.104
Amount of difference=Brain 50%.		Cord=40%.	

At the end of the Table the average of the cases examined twenty four hours after death is compared with a normal record (No. 51C, Table 7), and it is seen that there has been an increase in weight of about 50% in the brain and 40% in the cord, over and above the normal. There is no reason for insisting here on the constancy of exactly this amount of change, nor have I made experiments to determine in what manner it occurs, but it is evident that when left in the body for a day or more after death the central nervous system of the frog tends to increase in weight, and hence all examinations of it should be made as speedily as possible.

### IV. INFLUENCE OF WATER ABSORBED BY THE LIVING FROG ON THE WEIGHT OF THE BRAIN AND SPINAL CORD.

This capacity for change post-mortem as just described, would naturally suggest that normally the central nervous system

might be subject to considerable alterations in weight. As these normal alterations in a measure account for variations in the ratio of the weight of the brain to that of the spinal cord, we shall present such observations as we have made upon this point.

The amount of water in a frog is subject to rather wide fluctuation. In support of this statement, the following typical observation is offered. Six frogs, were freshly caught at 8 a. m., and divided into two groups of 3 each. These groups are designated as A and B.

At 9:30 a. m., August 12th.,

Group A. (3 frogs) weighed 132 grams.

“ B. (3 “ ) “ 125 “

Immediately after the weighing, each group was put in a shallow earthen dish about 30 cm. in diameter and the dish covered with a sieve. The dishes stood side by side, out of the direct sunlight, but exposed to a moist breeze.

The dish containing Group A. was dry, that containing Group B. had several layers of very wet filter-paper on the bottom. At the end of exactly seventy-two hours:

Group A. weighed 93.5 grams.

“ B. “ 121.0 grams.

Thus, both groups had lost weight during this time, which was to be expected, since they had been without food.

The loss in Group A was 29 %.

“ “ “ “ B “ 3.2 %.

The loss in Group B was due to lack of food and to defecation; in Group A, to similar causes combined with drying, hence the difference in loss amounting to 25.8 %, approximately represents the loss of water from Group A.

It is plain therefore, that a frog can lose a quarter of its weight by slow drying. After the last weighing, fresh water sufficient to cover the frogs above the level of the anus was put in both dishes. Within three hours after adding the water, Group A attained a weight of 134.5 grams, while the weight of Group B was not changed. Thus all the water which had been lost during three days of drying was regained by the three hours



exposure to a shallow bath. The water was taken up entirely by means of the part of the body immersed, as *frogs do not under any circumstances take water by the mouth.*

In other similar experiments, a slightly greater loss of water than that here recorded, caused the frog to die in convulsions, so that the loss above given, approximates the limit to which drying can be carried. The rate at which the water was absorbed was surprising, nevertheless the frogs remained in good condition, as was shown by the vigorous manner in which they jumped away when set free an hour later.

We conclude, therefore, that to obtain from a series of frogs records which shall be comparable, the frogs should be put in water for a few hours before they are examined and thus allowed to absorb the maximum amount of water which is normal for them.

The major part of the observations recorded in this paper were made on frogs kept in a large dark box beneath which flowed a small brook, the box being so arranged that they could be in or out of the water at will. It was assumed that they would all be equally moist, but the records show that even under these conditions some frogs are found much dryer than others.

The influence of the water absorbed, on the weight of the central nervous system and on the ratio of the brain weight to that of the spinal cord, is shown by the following observations, all made on one lot of frogs collected from the same locality, in the month of July.

They were made on successive days on groups of three frogs at a time. The group marked A "wet," had been in about half an inch of water for twenty-four hours previous to the examination. Those marked B "dry" had been in a dry dish for the same length of time.

TABLE 6.

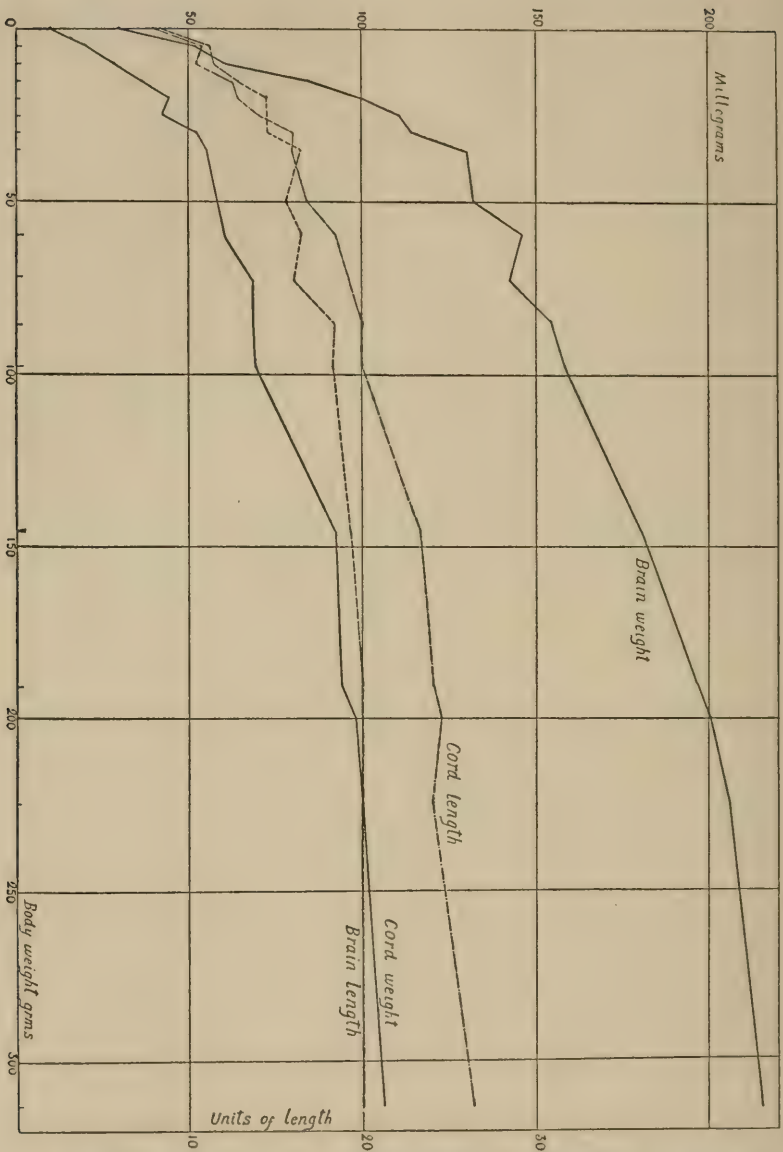
Average body weight in grms.	Average brain	Average spinal cord	
Frogs "wet."	Weight.	Weight.	Ratio.
Group A, 211, "wet."	.198	.097	2.04
Group B, 211, "dry."	.197	.084	2.34

Table 6 shows that the drying for twenty-four hours, causes a marked diminution in the weight of the cord, and at the same time affects the brain weight but little; consequently the ratio of brain weight to cord weight rises in the frogs as the result of drying for this length of time.

If the drying process is carried on for two or three days the brain also loses in weight and the ratio falls again. It will be noted that the "wet" body-weight is given for both groups in Table 6, as this is the only basis for a fair comparison between the two groups. The average body-weight in Group B after "drying" for 24 hours, was 176 grams. As the brain has been practically unaffected by the twenty-four hours of drying, these frogs appear to have *a high brain weight as compared with the weight of the body when dry*. The relation is of course explained by that which has just been stated.

In determining therefore, among frogs of the same size, the ratio of the weight of the brain to that of the spinal cord, we find the principal source of variation to depend on the amount of water taken up by the frog.

There are doubtless other sources dependent on irregularities in the growth of the central nervous system and probably also on modifications in the capability of the frog to take up water, depending in turn on the age of the frog, the state of nutrition and the season of the year; but there is no reason to think any of these conditions to be very important.



V. Chart I. Showing for Bull-frogs the weight of the brain and spinal cord in milligrams and the length, in millimeters, the records being arranged according to the increase in body weight.

## VI. EXPLANATION OF CHART I.

This chart exhibits the weight and length of the brain and spinal cord in frogs of different body-weights.

In constructing the curves, the unit of length which on the axis of abscissas represents one gram of body weight, on the axis of ordinates represents one milligram of brain or spinal cord weight. Two and a half of these units represent one millimeter in the curves illustrating the length of the brain and spinal cord. The chart is based on 18 cases taken from Table 7. The curves depend on single observations, and hence are liable to exhibit irregularities. The cases chosen were intended to give a curve falling within the extreme records.

By this method of selection the curve for the weight of the brain is most affected. It appears to be still rising, but Table 7 shows that the extreme weight indicated in the curve has been slightly surpassed twice by frogs weighing less than 250 grams.

On the other hand the largest frog obtained weighed 411 grams. The central nervous system had been left in the body twenty-four hours after death and therefore attained an abnormal weight which excluded it from the records. After the twenty-four hours in a refrigerator, the brain weight was .340 grams; the spinal cord weight was .168 grams.

Assuming that the brain weight is 50 % above the normal, and that the cord weight is 40 %, the corrected figures would be :

Brain weight,	.226 grams.
Cord weight,	.120 grams.

On comparing these results with the last entries in Chart 1, they suggest that there is still some opportunity for the brain to increase in weight slightly and the cord rather more and both of these suggestions are plausible.

## VII. METHOD OF OBSERVATION.

I have endeavored to examine a series of Bull-frogs from small to large. Very large frogs were not obtainable. Some were examined which were larger than those recorded, but in every case they had been the victims of broken



legs or of other damage, and were therefore rejected. For some reason, specimens weighing between 100 and 130 grams, were not found. It is possible that this was a mere accident, but it is also possible that at that weight, the frogs most readily escaped capture and hence were not brought in.

The observations recorded in Table 7 were made on Bullfrogs (*R. catesbiana*) during the summers of 1897 and 1898.

All the specimens were examined shortly after capture, only a few being kept more than ten days.

While awaiting examination, the frogs were protected from the light in boxes or dishes, for the most part so arranged that the animals could be in or out of water at will.

All weights were taken on balances sensitive to half a milligram. In referring to the tables, the records which involve the examination of the legs as well as the nervous system, are termed "complete" records, while those involving the nervous system only, are termed "partial records."

In every case, however, the "partial records" represent special observations and are not fragments of those intended to be complete.

The following account gives in detail, the manner in which the complete examination of a frog was made.

The frog was killed with chloroform or ether, and at once weighed entire.

The length was taken. The legs were next separated from the body and severed at the knee and ankle joints, thus dividing each leg into three segments. Each segment was placed immediately in a closed weighing bottle.

As a rule, the left leg was dissected first; it having been found that the weight relations of the two legs were not affected by the order in which they were dissected.

Before weighing the segments of the leg, the brain and spinal cord were exposed, their lengths taken, and then each removed to a small weighing bottle and weighed at once.

The sex was next determined. Lastly the weights of the stomach contents and the ovaries, when present, were ascertained and subtracted from the body weight as first taken.

The bottles containing the segments of the legs were then weighed separately. Next each segment was removed from the bottle and the bottle itself freed from any fluid that had collected in it. The skin, together with the bone (or bones), separated as completely as possible from the muscles and tendons, were returned to the dry bottle, which was weighed for the second time.

The difference between the first and second weighing gave the weight of the muscles of the respective segments.

The length of the leg bones was then determined. This measurement was made while the bones were fresh and moist, since they shorten on drying.

#### VIII. EXPLANATION OF THE ENTRIES IN TABLE 7.

From this table all derived numbers such as ratios and percentages have been purposely excluded. The derived numbers appearing in the body of the paper are, however, based on the records in this table, and can be verified by means of them.

As will be seen by examining the table, the various weighings were in centigrams or milligrams, as the case demanded, and lengths were taken in millimeters or tenths of a millimeter.

To facilitate the understanding of the Table 7, an explanation of each of the entries there found is added.

##### *Number.*

The number is given solely for the purpose of identifying the record.

The letter following it indicates the locality at which the frog was captured.

A. Lake Como—near Williams Bay, Wisconsin.

B. Fresh water Pond—near Oconomowoc, Wisconsin.

C. Several Ponds—near North Judson, Indiana.

\* Following the letter designating locality indicates that the record has been used in Chart 1.

##### *Sex.*

M. Male.

F. Female.

\* Following the letter designating sex indicates that the record has been used in a subsidiary table in the text.

*Body-weight.*

The total weight of the body as taken immediately after death, was corrected, if necessary, first by subtracting the weight of the stomach contents, when this was appreciable, and second, in females, by subtracting the weight of the ovaries, when these were mature enough to show black pigment.

*Length. (Lgth.)*

The frog was placed belly downward on the millimeter ruler and the legs given their greatest passive extension. The length was then taken in millimeters from a vertical touching the tip of the upper jaw to the end of the fourth toe of the longer leg. The two legs of the same frog often differ slightly in length.

*Weight of the muscles.*

Thigh—shank—foot. The leg was separated from the trunk by cutting first along the faint line which marks off the skin of the thigh from that of the trunk. The proximal attachments of all the thigh muscles were then cut with a scissors and the femur disarticulated at the hip-joint.

Similarly, a separation was made at the knee-joint and at the ankle.

Each segment thus consisted of the bone or bones belonging to it, surrounded by the muscles and associated tissues, and covered by the skin.

The weight of the tissues surrounding the bones and covered by the skin—that is, the muscles, tendons, nerves and vessels—is that recorded as the weight of the muscles. The records for the left leg always stand first in the table.

*Length of leg-bones.*

The bones were applied to a small metallic scale and the length read directly. In the case of the foot, the length was taken from the proximal end of the apophysis of the calcaneum to the tip of the fourth toe.

*Weight of the brain.*

The brain, within the limits given below, was raised on a narrow spatula, and the cranial nerves cut at their junction with it. The pia was for the most part left adherent. The choroid covering, the fossa rhomboidalis, and the hypophysis, were both removed, however, before the weight was taken.

*Weight of the spinal cord.*

The roots of all the spinal nerves were cut close to the cord itself, and this, within the limits given below, still covered with the pia, was then weighed.

*Length of the Brain.*

With spring compasses the measurement was made from the frontal end of the olfactory lobes to the caudal end of the calamus. The olfactory bulbs and tracts were thus excluded.

*Length of the spinal cord.*

The cord was measured in the same manner as the brain. The limits chosen were from the tip of the calamus to the point of attachment of the dorsal roots of the tenth spinal nerve.

The plane separating the brain from the cord thus fell a small fraction of a millimeter cephalad to the point of emergence of the first spinal nerve.

*Condition of the frog.*

When the condition is noted as "dry" it means that the frog was kept exposed to the air in a dry jar for twenty-four hours previous to examination.

In such cases the body-weight according to which the frog is entered in the table, is that taken *after the drying*. The "wet" body-weight would be higher.

The cases marked "wet" are from frogs so placed that for twenty-four hours previous to examination they could not get out of the water.

The cases which bear no indication were undetermined, and although the proportion of water in them probably varies in no small degree, they were from frogs so placed that they could be in or out of water at will.

That the "dry" frogs stand too low in the table owing



to their being entered according to the "dry" body-weight, is shown by the fact that in seven out of a total of eight cases they exhibit a brain-weight *greater* than that of the next heavier frog.

## IX. TABLE OF RECORDS.

Table 7.

No.	Body.			Weight of Muscles.			Length of Bones			Weight.		Length.		Con- dit'n
	Sex	Weight	Lgth	Thigh.	Shank.	Foot.	Femur.	Tibia.	Foot.	Brain	Cord.	Brain	Cord.	
1 B*	F*	1.32	56	-----	-----	-----	-----	-----	-----	.025	.009	8.4	8.	
2 A	M*	3.53	87	.321 .325	.107 .108	.060 .062	15.2 15.2	16.8 16.8	26. 26.	.042	.016	10.	9.1	
3 B	M	4.17	90	-----	-----	-----	-----	-----	-----	.043	.015	10.8	10.	Dry
4 B	M	4.28	91	.364 .371	.116 .107	.066 .068	15.8 15.8	17. 17.	26.8 26.5	.043	.019	10.3	10.8	
5 B	F	4.78	91	-----	-----	-----	-----	-----	-----	.050	.017	10.5	10.3	Dry
6 B	M	5.02	93	.438 .450	.132 .141	.081 .088	16.8 16.6	18.2 18.4	28.2 28.3	.045	.017	11.	10.7	
7 B	F	5.04	96	-----	-----	-----	-----	-----	-----	.053	.019	11.5	10.1	Dry
8 B*	M	5.38	95	.452 .467	.148 .153	.083 .084	17.7 17.7	18.4 18.4	28.2 28.2	.052	.020	11.	11.1	
9 A	F	8.75	127	.846 .831	.268 .260	.153 .152	22. 21.7	23.6 23.4	37.3 37.5	.062	.026	12.9	12.2	
10 A*	M	10.50	119	.975 .978	.323 .334	.175 .175	20.5 20.5	23.8 23.5	36. 36.	.060	.026	11.7	10.5	
11 A	M	11.29	121	1.041 1.028	.325 .325	.173 .168	21.3 21.3	23.3 23.3	36.3 36.3	.065	.030	11.4	10.3	
12 A	M	11.37	125	1.081 1.114	.393 .381	.192 .191	22.2 22.2	25. 25.0	37.4 37.2	.075	.033	12.8	12.	
13 A	F	13.77	136	1.372 1.314	.450 .456	.255 .258	24. 24.	26.4 27.	42.4 43.	.081	.035	13.5	12.5	
14 A*	F	16.03	145	1.764 1.694	.595 .572	.317 .319	24.8 24.8	27. 27.	43. 43.	.085	.037	12.8	12.1	
15 A*	M	20.33	159	1.620 1.673	.592 .588	.335 .320	28. 28.2	30.5 30.5	48. 49.	.100	.044	14.2	12.6	

No.	Sex	Body.		Weight of Muscles.			Length of Bones			Weight.		Length.		Con- dit'n
		Weight	Length	Thigh.	Shank.	Foot.	Femur.	Tibia	Foot.	Brain	Cord.	Brain	Cord.	
16 A*	M	27.33	167	2.94 2.95	1.054 1.035	.535 .512	30. 30.2	32.4 32.5	52.2 51.	.110	.043	14.5	14.	
17 A	F	27.51	173	3.00 2.97	1.127 1.132	.622 .609	30.3 30.8	33.5 33.5	52.8 52.8	.121	.049	15.2	17.4	
18 A*	M	32.95	184	3.28 3.15	1.182 1.173	.640 .570	32.1 31.	33.2 33.	52.5 48.	.114	.051	14.5	16.	
19 A	F	36.32	182	3.85 3.81	1.348 1.348	.627 .620	31.5 32.	34.7 34.7	54.5 54.5	.107	.046	14.3	15.1	
20 A*	F*	37.46	188	3.86 4.09	1.395 1.455	.749 .741	34.5 34.8	37.4 37.8	58.4 58.	.130	.055	16.2	16.	
21 A	M	49.50	192	4.56 4.78	1.560 1.552	.711 .727	32.5 32.5	36.2 36.3	56. 56.4	.127	.054	16.1	15.8	
22 A*	F	49.82	202	4.98 4.79	1.632 1.604	.857 .879	34. 34.	37.3 37.8	58. 59.	.132	.057	15.8	16.8	
23 A	F	50.43	203	5.21 5.18	1.801 1.811	.896 .880	34. 34.	37.2 37.2	56.5 56.5	.138	.062	16.	17.8	
24 A	M	51.77	200	5.66 5.60	1.863 1.881	.931 .930	35. 35.2	38. 38.5	60.5 60.3	.143	.058	16.5	17.	
25 A	F	58.46	210	6.01 5.83	1.935 2.020	1.035 1.019	36.2 36.	38. 38.	59.5 59.4	.123	.061	15.5	18.	
26 A*	F	60.12	211	6.74 6.77	2.331 2.365	1.113 1.115	37. 37.	41.8 41.8	63.2 63.	.145	.060	16.5	18.5	
27 A	F	66.67	218	7.07 7.08	2.392 2.375	1.096 1.115	37.5 37.5	40. 40.	62. 62.	.143	.072	16.1	18.3	
28 B*	F	73.05	231	6.92 7.19	2.120 2.420	1.707 1.575	40.5 40.5	41.5 41.5	69.2 69.2	.143	.069	16.	19.2	
29 B	M	76.69	231	7.20 7.37	2.500 2.528	1.573 1.645	41. 41.	42.3 42.	71.6 71.8	.160	.073	17.2	20.4	
30 B*	M	87.05	231	9.08 8.89	2.839 2.896	1.763 1.790	42.5 42.5	44. 43.	74. 73.2	.154	.069	18.2	20.	
31 B*	M	98.00	240	-----	-----	-----	-----	-----	-----	.157	.069	18.1	20.	
32 C	M	138.50	275	-----	-----	-----	-----	-----	-----	.175	.080	19.	19.7	Dry
33 B	M	144.50	280	12.81 12.81	4.175 4.175	2.660 2.660	49.5 49.5	51.5 51.5	86.2 86.2	.169	.086	19.	23.2	†
34 C	M	146.30	269	-----	-----	-----	-----	-----	-----	.188	.084	19.4	21.6	Dry

†Left leg only examined.

No.	Sex	Body.		Weight of Muscles.			Length of Bones			Weight.		Length.		Con- dit'n
		Weight	Lgth	Thigh.	Shank.	Foot.	Femur.	Tibia	Foot.	Brain	Cord.	Brain	Cord.	
35 C*	F	146.70	284	-----	-----	-----	-----	-----	-----	.181	.092	19.3	23.7	Wet
36 B	F	146.90	275	-----	-----	-----	-----	-----	-----	.194	.085	19.4	20.9	
37 C	F	162.80	272	-----	-----	-----	-----	-----	-----	.203	.087	20.1	21.3	Dry
38 C	F	169.50	275	-----	-----	-----	-----	-----	-----	.176	.086	18.9	22.8	Wet
39 C	M	184.60	284	-----	-----	-----	-----	-----	-----	.191	.096	20.	22.6	Wet
40 C	F	188.15	300	-----	-----	-----	-----	-----	-----	.219	.090	20.4	22.8	Dry
41 A*	M	191.76	313	19.94 19.54	6.747 6.805	4.205 4.220	56. 55.6	58. 58.2	97. 97.5	.196	.094	20.	24.	
42 C*	M*	199.10	312	18.30 18.75	5.910 6.020	3.865 3.925	56.5 53.5	55. 55.3	92. 92.5	.200	.099	20.	24.3	
43 C	M	206.70	284	-----	-----	-----	-----	-----	-----	.182	.091	18.2	22.	Wet
44 C	M	212.50	304	18.23 18.52	6.070 6.185	3.947 4.362	53.5 53.5	55. 55.	93. 93.2	.207	.099	18.	25.2	
45 A	F	221.94	310	21.64 20.54	7.204 7.157	4.708 4.366	56.3 55.5	58.1 57.9	93.2 94.	.221	.100	21.5	23.2	
46 C*	F	225.20	303	-----	-----	-----	-----	-----	-----	.205	.100	20.4	23.5	Wet
47 C	M	230.60	315	-----	-----	-----	-----	-----	-----	.186	.085	20.	22.5	Dry
48 A	M	233.79	344	22.92 23.04	7.377 7.492	5.013 4.888	62. 62.	64.2 64.2	105.4 104.2	.228	.101	21.	25.2	
49 C	F	241.85	312	-----	-----	-----	-----	-----	-----	.215	.107	20.9	24.4	Wet
50 B	M	244.60	313	-----	-----	-----	-----	-----	-----	.196	.096	19.6	25.8	Wet
51 C	F*	272.10	340	-----	-----	-----	-----	-----	-----	.202	.104	21.2	26.	Wet
52 C*	M*	313.50	343	28.57 29.06	8.945 8.967	5.905 5.663	60. 60.	61. 61.	102.5 102.5	.215	.106	20.	26.5	

## X. GROWTH.

At the present time observations on the weight of frogs at different known ages, are still wanting.

It seems probable that enlargement occurs in the frog during the late spring and early summer, and by analogy, we should expect the increase in length to occur before the most active increase in weight. These statements, however, await demonstration.

From the examination of Chart 1, it is at once evident that the weight of the central nervous system increases so long as the weight of the entire body increases. The form of the curve also shows that after the frog has attained a body-weight of about 75 grams the increase in the weight of the central nervous system becomes slow.

Although we have no data as to the time relations of these growth changes, something can be inferred from the foregoing records as to the axes along which the enlargement takes place.

To illustrate this, there is given below in Table 8, the weight in milligrams of an average millimeter of both brain and spinal cord. Also in another column the square root of the number representing this weight.

The cases chosen are the same as those in Table 1.

TABLE 8.

Body weight	Weight in mgms. of 1 mm. of brain	Square root of preceding number	Weight in mgms. of 1 mm. of spinal cord	Sq. root of preceding number
1.32	3.0	1.7	1.1	1.0
3.53	4.2	2.0	1.7	1.3
37.46	7.9	2.8	3.0	1.7
199.10	10.0	3.1	4.0	2.0
313.50	10.7	3.3	4.0	2.0

For the purpose of comparison such as is made in Table 8, we assume the mass of the brain and spinal cord to be moulded in the form of a prism with a square base, the long axis of which geometric figure is assumed to be equal to that of the part observed. In such a figure, each millimeter taken on the long axis will have the same weight.

In Table 8, the weight of one millimeter of brain or spinal



cord thus moulded, is given for the frogs of several sizes, and assuming the specific gravity of the nerve substance to be unity (it is probably about 1.03), the square root gives the length in millimeters of each side of the mass. For under the conditions stated 1 cubic millimeter weighs 1 milligram.

Since the weight of the average millimeter increases with the increase in the size of the frog, it is plain that enlargement both in the brain and the spinal cord is taking place in planes at right angles to the long axis, as shown in columns 3 and 5, Table 8.

If the enlargement had been proportional along all the axes, then (the natural geometric form of the brain and cord remaining the same, as is practically does), the weight relations in any two frogs would be proportional to the cubes of the respective long axes of their central nervous system.

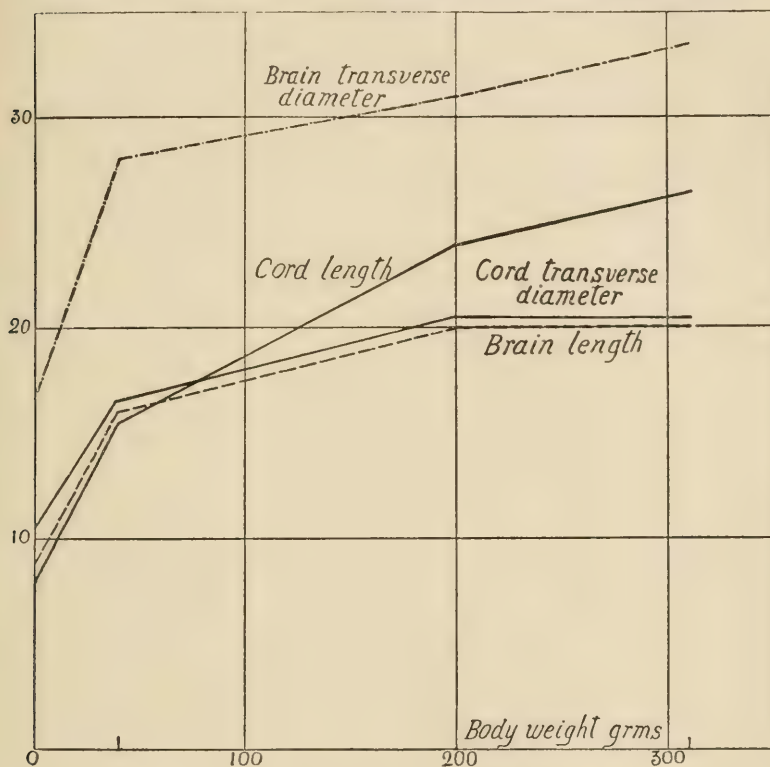
Applying this test to the limiting cases in Table 8, we obtain the following:

Body weight.	Length of brain. mm.	Length of spinal cord. mm.
1.32	8.4	8.0
313.50	20.0	27.6

On comparing the cubes of these respective lengths, it appears that the increase should be 15 fold for the brain and 40 fold, for the spinal cord if the enlargement along all the axes had been proportional. The actual weight relations as shown in Table 2, indicate, however, an increase of only 8 fold for the brain and 12 fold for the spinal cord. From these data several conclusions can be drawn. First that the increase in the long axis of the brain and spinal cord is more rapid than in the other axes, and second, that enlargement in planes at right angles to the long axis is more slowly accomplished in the brain than in the spinal cord. Moreover, in both localities, the latter change is more marked during the early stages of growth. The accompanying Chart 2, based on the length of the cord and length of one side of the corresponding millimeter segment, shows these relations better than the table.

## XI. CHART 2.

Chart showing growth changes in the brain and spinal cord.



## XII. EXPLANATION OF CHART.

In this chart, four cases alone are plotted. The second record in Table 8, being omitted for convenience. One unit of length on the axis of ordinates corresponds with 1 millimeter in the length of the Brain and Spinal Cord. Ten units are taken to correspond to one millimeter in the transverse diameters. On the axis of abscissas, 1 unit corresponds to 10 grams of body-weight. In the Chart the curve for the cord's transverse diameter has been displaced upwards to prevent confusion. It should begin exactly at 10 and end at 20.

This curve is to be interpreted as follows: The steeper the curve the greater is the relative increase in size along the axis

which is indicated by it. Thus the curve for the transverse diameter of the brain indicates that growth is still going on there, when it has nearly stopped in the long axis. For the spinal cord, the reverse relation is shown.

#### XIII. OBSERVATIONS ON THE LEGS.

The results under this head can be stated in a condensed form.

There are 33 complete records given in Table 7.

For convenience these are here arranged in three groups:

Group I. 16 cases including No. 20 A.

Group II. 13 cases including No. 41 A.

Group III. 4 cases including No. 52 C.

#### XIV. WEIGHT OF THE MUSCLES OF THE LEGS.

As compared with the weight of the entire body the weight of the muscles of the legs is as follows:

TABLE 9.

	Proportional weight of the muscles of both legs
Group I.	30.5%
Group II.	29.3%
Group III.	28.6%

This indicates a slight but steady decrease in this proportion. The weights of the muscles of the right and left sides are rarely alike, but there is no evidence of a difference predominantly in favor of one side.

When the weight of the muscles of the thigh is compared with that of the muscles from the remainder of the leg, the relation is found to be nearly constant.

TABLE 10.

	Ratio of Weight of muscles of thigh.	To weight of muscles of the remainder of the leg.
Group I.	1.867	1
Group II.	1.869	1
Group III.	1.857	1

In both instances the individual variations are comparatively small, so that the averages are applicable to special cases.

## XV. LENGTH OF LEG BONES.

The length of the leg bones taken together, as compared with the length of the entire frog is given in Table 11.

TABLE 11.

Percentage of the entire length of frog  
represented by the sum of the lengths of  
the leg bones.

Group I.	66.8%
Group II.	65.7%
Group III.	66.4%

In Table 12, are given the percentage values of the length of the three sets of bones, the sum of all three being considered equal to 100%. For the definition of "Foot" as here used see section VIII, heading, Length.

TABLE 12.

	Proportional lengths of		
	Femur	Tibia	Foot.
Group I.	26.6	28.6	44.8
Group II.	26.1	27.7	46.2
Group III.	26.7	27.6	45.7

From the foregoing, it is concluded that the weight of the leg muscles as compared with that of the entire body is the only relation that varies regularly with the size of the frog, and even in that case, the variation is small.

In other respects the weight and length relations of the frog's leg are similar in frogs of all sizes. The general conclusions from these observations are stated in the summary at the beginning of the paper.





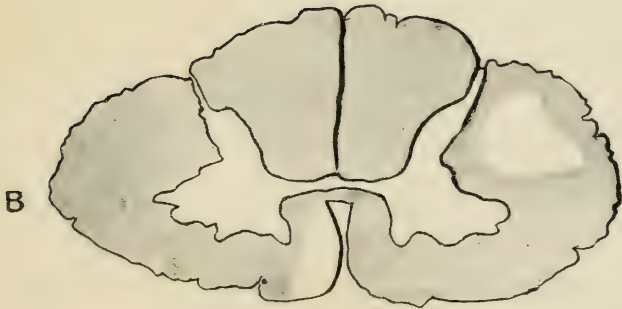






Fig. 8.

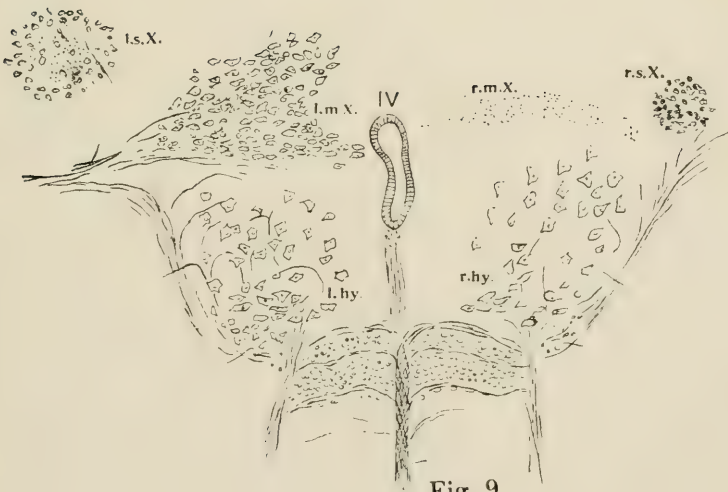


Fig. 9.





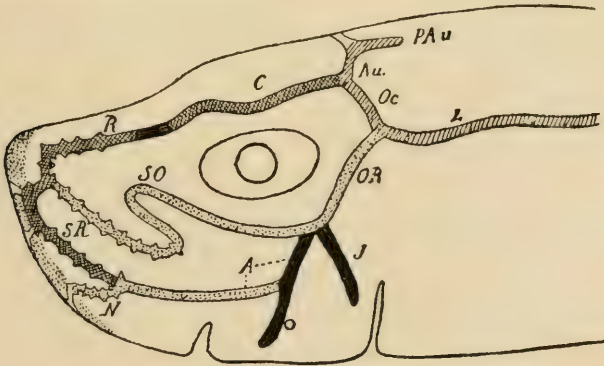
## LITERARY NOTICES.

### MORPHOLOGY.

#### Cranial Nerves of *Chimaera*.<sup>1</sup>

This research forms a welcome and valuable addition to our present knowledge of the cranial nerves of this important form. Its appearance, together with the author's previous communication in the *Anatomischer Anzeiger* (Bd. XII, p. 172, 1896), is also timely inasmuch as it will probably prevent additional confusion on the subject of the cranial nerves of fishes which might otherwise arise from Collinge's work on the same subject. Owing to the nature of the material the research was made entirely by means of dissection.

After a good historical review of the literature on the nervous system of *Chimæra*, the author passes to a consideration of the classification of sensory canals which contains an interesting discussion, referred to more in detail below, of the independent character of the nerves innervating the sensory canals. Cole classifies the canals in accordance with their innervation into (1) superficial ophthalmic, (2) buccal, (3) hyomandibular, and (4) lateralis.



The accompanying figure indicates these different canals by differences in shading, the different parts according to Garman's nomenclature being indicated by letters.

<sup>1</sup> On the Cranial Nerves of *Chimæra monstrosa* (Linn.), with a Discussion of the Lateral Line System and of the Morphology of the Chorda Tympani, by FRANK J. COLE. *Trans. of the Royal Society of Edinburgh*, Vol. XXXVIII, Part III, (No. 19).

(1) Supra-orbital canal (superficial ophthalmic, cross hatched — the black segment is the portion innervated by the profundus) = cranial (*C*) + rostral (*R*) + sub-rostral (*SR*).

(2) Infra-orbital canal (buccal + otic, dotted) = orbital *OR* + sub-orbital (*SO*) + portion of angular (*A*) + nasal (*N*).

(3) Hyomandibular or Operculo-mandibular canal (external mandibular, black) = remainder of angular (*A*) + oral (*O*) + jugular (*J*).

(4) Lateralis canal (lateralis, oblique shading) = lateral (*L*) + occipital (*Occ*) + aural (*Au*) + post-aural (*PAu*).

Nothing new is described with respect to the olfactory and optic nerves.

The *third nerve* after giving off a branch to the superior rectus divides into superior and inferior branches, the former proceeding dorsal to the optic and also the inferior rectus and inferior oblique to the internal rectus which it innervates. The ventral branch near its origin gives off a fine radix brevis which is joined by a radix longa from the ophthalmicus profundus. At their junction lies the ciliary ganglion which gives off two ciliary nerves. This ganglion thus does not correspond to the group of ganglion cells on the ventral branch of the III and described by Schwalbe as the ciliary—probably both are present.

The profundus also gives off some ciliary nerves.

The *Patheticus* has a typical exit and course. It proceeds under cover of the superficial ophthalmic for a portion of its course to the superior oblique.

The *Abducens* arises by six rootlets at a level slightly behind the dorsal root of the VIIth and a little in front of the root of the glossopharyngeal. It runs under the Vth and VIIth, closely applied to the former and enters the orbit by a foramen hidden by the Vth and VIIth trunk. It, of course, innervates the external rectus.

The *Trigeminus* is entirely distinct from the facial, arising by two closely applied roots from the side of the medulla. Whether the anterior smaller root is the root of the profundus could not be anatomically shown by dissection. As the V enters the orbit, it gives off a fairly large bundle to the VII. This bundle divides, one part accompanying the inner buccal, not further traceable, and the larger part accompanying the outer buccal, a portion separating again from the latter. This is stated to constitute "the *only* confusion or mingling between the facial and trigeminal nerves in Chimæra." The principal branches of the Trigeminus are the Profundus (*P*), the Superficial Ophthalmic

(S.O.V.), the Maxillary (Mx.) (pre-branchial), the Mandibular (Mn.) (post-branchial) and the Pharyngeal, or visceral.

The profundus arises from the trunk of the V, but has its separate ganglion. One of the most interesting facts in connection with it is that it gives off a small branch while crossing the orbit which innervates two sense organs of the supra-orbital canal. While passing from the orbit through the cartilage of the cranium, the profundus becomes "wrapped around the ventral surface of the superficial ophthalmic of the facial. It can be separated from this for a short distance, but finally becomes inseparably fused with it." It is somewhat difficult to reconcile this statement with the one first quoted respecting the absence of confusion between the V and VII nerves. After its fusion with the ophthalmicus superficialis VII, the profundus gives off a thin nerve to the outer surface of the inner wall of the nostril which is regarded as probably corresponding to the motor division of the profundus found in Cyclostomes. The profundus also gives off a twig to the ciliary ganglion.

The superficial ophthalmic branch of the V may in some cases be entirely distinct from the superficial ophthalmic branch of the VII and does not innervate any organs of the lateral line. The maxillary innervates the masseter and labial and nasal muscles, also the skin and the walls of the nasal sac and mouth. It gives off the large pharyngeal or visceral branch which innervates a portion of the mucous membrane just inside the mouth. The mandibular innervates the masseter and muscles of the lower lip (also the skin?), and probably parts of the mouth.

In a comparison with the results of Pinkus in *Protopterus*, Cole points out that in *Protopterus* the profundus does not fuse with the superficial ophthalmic of the VII and that its cutaneous distribution is therefore an ascertained fact and not a surmise. He also points out the interesting correspondence of the three "accessory cutaneous branches," described by Strong in *Amphibia*, to the bundles leaving the V in *Chimæra* and accompanying the buccal VII.

The results of Cole's examination of the *Facialis* are especially interesting and exhibit a gratifying agreement with the views arrived at by workers on other forms. The facial is, very properly, divided into the facial proper and the lateral line nerves. The whole facial nerve arises by three separate roots whose arrangement can be readily understood from the accompanying reproduction of one of Cole's figures. The roots of the V are also shown. VII<sub>1</sub>, arising ventrally, from the medulla (Mo), is the root of the superficial ophthalmic VII (S.o.VII),





It is evident from the above, then, that the lateral line portion of the VII, arising by two roots, has three main branches: the superficial ophthalmic, the buccal and the external mandibular, and that the facial proper, arising apparently by a single root, has also three main branches: a pharyngeal or visceral (palatine), a pre-branchial (which Cole regards as the chorda tympani) and a post-branchial.

One fact that attracts attention here is the extremely ventral position of one of the lateral line roots, being considerably ventral to the auditory. Whether this really offers any morphological difficulties can only be determined after a microscopical examination of the medulla. It may be further pointed out that the root of the facial proper—VII<sub>3</sub>—is almost unquestionably a compound root. Sections of the medulla at this level will in all probability reveal the fact that a portion of its fibers are motor, arising from a motor nucleus, and a portion (sensory) belong to the “fasciculus communis” system. The former would pass into the post-spiracular, the latter principally into the palatine and pre-spiracular branches.

The palatine nerve innervates the roof of the mouth and the teeth of the upper jaw. The pre-spiracular branch pierces the cranium to the external wall of the pharynx, proceeds to the lower jaw, giving off pharyngeal branches, and is distributed to the outer wall of the pharynx and to the ventral part of the inner wall of the pharynx as far mesad as the mid-ventral line. It also receives an anastomosing branch from the post-branchial. The post-branchial nerve divides into two portions. One of these innervates the extensor of the hyoid arch and gives off a twig which anastomoses with the pre-spiracular. The other division supplies the superficial muscles of the opercular fold and of the body wall overlying the gill clefts in front of the opercular fold, and between the latter and the mouth.

The superficial ophthalmic nerve innervates the 27 (in the specimen examined) organs of the supra-orbital canal with the exception of the 12th and 13th, which are the two above referred to, which are supplied by the profundus. It also innervates the superficial ophthalmic group of ampullæ. Its large ganglion lies in the wall of the cranium. The buccal arises, as above mentioned, apparently exclusively from the dorsal lateral line root, though the possibility of its receiving some fibers from the other lateral root is not entirely excluded. Its large ganglion likewise lies in the wall of the cranium. On entering the orbit, it gives off the ramus oticus which supplies the first 8 sense organs of the infra-orbital line and the most ventral of the ampullæ opening upon the surface by the large occipital pores, the remainder of these ampullæ being

innervated by the superficial ophthalmic. The buccal then divides into two large bundles. One of these, the inner buccal, gives off 22 branches supplying the inner buccal group of ampullæ and the 26 sense organs of the dorsal division of the infra-orbital line. The other bundle, the outer buccal, supplies the 14 sense organs of the ventral division of the lateral line and the outer buccal group of ampullæ. The ampullæ of this latter group are only about half the size of those of the inner buccal and superficial ophthalmic groups, but are larger than those of the mandibular group. The external mandibular divides into two parts, a posterior and an anterior. The posterior, which probably contains also some fibers from the facial proper—as it anastomoses with the post-branchial VII and sends twigs to the skin—innervates a small and probably degenerate group of ampullæ and the 7 sense organs of the posterior division of the hyomandibular canal. The anterior part supplies the 11 organs of the anterior division of the hyomandibular canal and the mandibular group of ampullæ. These latter ampullæ are not compound but simple and kidney-shaped.

The lateralis, which Cole includes in the VIIth nerve (see below), “arises somewhat in front of and on a slightly higher level than the roots of the vagus, and partly in front of the glossopharyngeal.” It is readily shown by dissection to be quite independent of the vagus. While in the cranium, it gives off a dorsal twig which unites with another from the ganglion and innervates the occipital portion of the lateralis canal. The main nerve proceeding backwards, expands into the large lateralis ganglion immediately after passing through the vagus foramen. It then courses backward parallel to the lateralis canal which it innervates for the whole of its length. This independent origin of the lateralis, it may be noted, agrees with the condition found by others in Elasmobranchs (Ewart), Teleosts (Herrick), Dipnoi (Pinkus) and Amphibia (Strong) and Cole himself vouches for it in *Raia*, *Scyllium*, *Acanthias*, *Heptanchus*, *Læmargus* and *Torpedo*.

Besides noting the presence of a hitherto undescribed hard otolith in the sacculus, no points of special interest were found in connection with the auditory nerve which apparently is similar to that of *Læmargus*.

“The ninth nerve in *Chimæra* arises from the medulla by one large root and two small rootlets below and under cover of the anterior rootlets of the lateralis, as in all cartilaginous fishes. It passes through the cranium by a separate foramen and immediately expands into an obvious ganglion. From this ganglion the very fine dorsal branch arises, which does not, however, innervate any sense organs of the lateral line but passes straight upwards to the skin of the occipital re-

gion." The glossopharyngeal has, besides, the following branches: (1) Pre-branchial which innervates the first demi-branch and the ventral wall of the pharynx. (2) Post-branchial runs along the base of the second demi-branch, reaches the pharynx and there divides. (3) and (4) Accessory skeletal branches. Under this name Cole describes branches, hitherto overlooked, of the IXth and Xth nerves supplying the visceral arches themselves and quite distinct from the pre- and post-branchial nerves. They may arise from either of these two latter nerves or may have a distinct origin. They are always closely applied to the arches they supply and frequently pierce the cartilage. Cole finds them also in cartilaginous fishes. There are two belonging to the IXth nerve in *Chimæra*, one coursing along the anterior edge of the first branchial arch and the other along its posterior edge. (5) Motor branch to the large levator muscle attached to the anterior face of the hyoid arch and also to a small muscle attached to its posterior face. (6) Pharyngeal or visceral branches, peculiar in *Chimæra*, since there are always at least two to every branchial nerve. The glossopharyngeal has three, thus constituting five visceral branches including the continuations of the pre- and post-branchial nerves.

The vagus is a complex composed of four perfectly independent nerves, termed vagus 1, 2 and 3 and the intestinal. Vagus 1 has the following branches: (1) Pre-branchial to the third demi-branch and pharynx. (2) Post-branchial to the fourth demi-branch and pharynx. (3) Extra-branchial arising from one of the accessory skeletal branches and distributed to the fourth demibranch. (4) and (5) Two accessory skeletal branches running along the anterior and posterior edges of the second branchial arch. (6) Motor branch similar to that of the IX, but arising from the pre-branchial. It is distributed to the same muscle as the anterior division of the motor branch of the IX. (7) Visceral proper, one branch of which supplies the levator of the first branchial arch and the other is distributed to the pharynx. (8) Accessory visceral branch, most ventral of all and associated with the pre-branchial. It "ends in the dorsal internal surface of the pharynx, the external surface of the same part of the pharynx being innervated by the accessory visceral branches of the IX."

The branches of vagus 2 are in the main the same. Three accessory skeletal branches are described and three accessory viscerals, two of which arise from the pre-branchial. The motor branch, a very fine nerve, innervates a "longitudinal band-like muscle lying over the gill arches a little to one side of the mid dorsal line." A branch of the visceral proper innervates the levator of the second arch. Vagus 2



gives off, just distal to its ganglion, a slender dorsal branch which soon bifurcates and is distributed to the skin of the occipital region. Vagus 3 presents some further variations which need not be noted here. Its post-branchial supplies the eighth or last demi-branch. The intestinal division of the vagus arises as its most posterior root and soon after leaving the cranium expands into an obvious ganglion. It splits up forming a plexus on the pharynx and proximal part of the oesophagus. Some bundles reunite and again break up to form a plexus on the distal part of the oesophagus and the stomach which was traced as far as the spiral valve. Both plexus lie on the circular muscles of the oesophagus and stomach, beneath the pigmented serous coat. A very slender nerve was with much difficulty traced on to the wall of the sinus venosus and this was the only cardiac branch of the vagus found.

To the description of the intestinal nerve is appended an interesting discussion of Shore's results on the vagus of the skate. Shore's views, which follow Gaskell's lines, probably require some revision in view of the results of researches upon the sympathetic and cerebro-spinal ganglia by means of the Golgi and Ehrlich methods. It is interesting to note that here also we find a somatic cutaneous branch so that the vagus cannot be regarded as purely splanchnic (excluding, of course, the lateral line system). This somatic element has been shown to be present in some amphibia, in certain teleosts by Herrick and, further, Kingsbury has shown that in the medulla of several teleosts we have certain contingents separating from the spinal V and passing out with vagus roots, thus indicating the probable existence of cutaneous branches. The writer of this review can, from his own observation, add *Hiatula onitis* to this list.

The anterior spinal nerves have no dorsal roots and pass through the cranium. There are numerous rootlets which unite into two main nerves, emerging by three foramina. These two nerves unite to form the brachial nerve. The first "cranial spinal," as these two nerves are termed, arises by seven rootlets which unite just outside the cranium and sends a dorsal branch up to the skin. The second cranial spinal arises by six rootlets which form two roots which remain in the main distinct but interchange fibers just outside the cranium, at which point two dorsal branches are given off to the skin. The brachial nerve formed by the union of these two cranial spinal nerves is distributed to the pectoral fin and sends a branch to the muscles of the last or fifth branchial arch.

In his discussion of the independent character of the lateral line system, Cole marshals the arguments in favor of this view more clearly

and convincingly than has hitherto been done. Reviewing the development of our knowledge in the gradual exclusion of the Vth from the innervation of the lateral line organs, he points out that the scheme of their innervation given by him (*vide supra*) has been shown to apply to all classes in which the lateral line system exists, if we take the most careful researches as a guide e. g. Holocephali (Cole), Elasmobranchs (Ewart), Teleosts (Pollard—Siluroids e. g. Clarias, and Auchenaspis and we should now add Herrick's researches on Menidia as most conclusive of all as to the condition in Teleosts), Ganoids (Allis), Dipnoi (Pinkus) and Amphibia (Strong). He summarises the proofs that "the lateral line system is a distinct formation innervated by a single and specially developed system of nerves" as follows:

(1) Their distinct and characteristic development from the skin and not "like the true cranial nerves" from the neural crest (Pollard, Beard, Frierip, Kupffer).

(2) The development of the canal organs by the splitting of a single organ (Beard).

(3) The total disappearance of the lateral line nerves when the organs disappear, as in the metamorphosis of the frog (Strong).

(4) "The tendency on the part of the lateral line nerves to arise both in the embryo and in the adult by the splitting of a single trunk" (Amphibia—Strong, Siluroids—Pollard, Elasmobranch embryos—Van Wijhe, Beard, Laemargus—Ewart). It may be remarked here, as Cole points out in a later paper,<sup>1</sup> that this condition is often secondary.

(5) The common origin (or rather terminus or center) of the lateral line nerves in the brain.

(6) The fact that each lateral line nerve has its own ganglion distinct from the ganglion of the cranial nerves *sensu strictu*.

The grounds above adduced by Cole are of great strength and establish a strong presumption against apparent contradictions such as are found in the description of the innervation of canal organs in certain cases by other nerves than those of the lateral line system. Such exceptions obviously require a careful consideration and this Cole devotes to two of these cases which have been apparently clearly observed. The first is the case, observed by Cole himself, of the innervation of two sense organs of the supra-orbital canal by twigs from the profundus. Cole thinks, very properly, that we may assume here on *a priori* grounds, and pending a complete microscopical examination, that

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<sup>1</sup> Reflections on the Cranial Nerves and Sense Organs of Fishes. *Trans. Liverpool Biological Soc.*, Vol. 12, 1898.

some fibers of a lateral line nerve accompany the profundus. The second case discussed by Cole and considered by him more difficult of explanation, is the innervation of a canal organ by a twig from the glossopharyngeus in Elasmobranchs, Teleosts and Ganoids. Cole thinks the explanation in the case of the profundus inapplicable here where so many different groups are involved. It may be pointed out here that the difficulty in this last case has been materially lessened by two more recent researches. We know from Kingsbury's researches that in *Amia* the glossopharyngeus is re-enforced by fibers from the root of the N. lateralis and it is only reasonable to suppose, as Kingsbury points out, that those are the fibers which compose the twig from the glossopharyngeus to a canal organ. Furthermore, in an examination of serial sections through the head of *Squalus acanthias*, the writer of this review found that here also fibers passed from the root of the N. lateralis, near its exit from the brain, to the glossopharyngeus. These fibers could be traced as a component of the glossopharyngeus until they separated outside the auditory capsule as a twig to a canal organ. Thus the true state of affairs in this apparent exception really greatly strengthens the view as to the specific character of the innervation of the lateral line organs. It can hardly be doubted that this explanation will be found to apply to the other forms mentioned by Cole. As a slight correction of a statement by Cole that Strong failed to demonstrate this twig in amphibia it may be stated that a twig corresponding to this was shown to arise from the vago-glossopharyngeal complex in the tadpole but that its fibers were found to be derived here also from the root of the N. lateralis.

The complete exclusion of all the cranial nerves except the special lateral line roots from the innervation of this system of organs being a point of very considerable importance and one to be determined with certainty as a necessary preliminary to further deductions, it may be pointed out here again (*vide supra*) that Cole, notwithstanding assertions apparently to the contrary, has not yet made out a complete case from actual observation. For example, we have that extensive fusion of the profundus with the lateral line nerve, the ophthalmicus superficialis portio facialis. The exact character of the twigs given off beyond this point has not been ascertained from actual observation i. e. it is not demonstrated that those twigs which supply the canal and ampullary organs are solely derived from the facial portion of the joint nerve. This fusion is commonly met with in Elasmobranchs and it has not apparently been completely analyzed there. The fusion of fibers from the root of the buccal with the hyomandibular described by Cole in



Chimæra also requires further analysis, as well as some minor fusions, to completely establish from observation as well as from inference the exclusive innervation of this system by these roots.

While Cole must be regarded as justified in thus strongly upholding the independence of the lateral line nerves, yet his corollary that the lateralis must not only be associated with the other lateral line nerves but also "considered a component of the VIIth cranial nerve" is open to the criticism made by Herrick—there is really no more ground for considering the lateralis "VIIth" than the preauditory lateral line roots "IXth" or "Xth." It would be more justifiable to extend the term "VIIIth" to cover the whole complex (somewhat as Mayser suggested) if the doctrine in question must be indicated in a numerical rearrangement, but the best course is that suggested by Herrick, viz, to simply denominate the whole complex the acustico-lateral system. There are however problems still awaiting solution before any fundamental remodeling of cranial nerve nomenclature can be undertaken—if indeed it is advisable that it should be undertaken.

One fact that attracts attention in looking at Cole's figures of the preauditory roots of the facial is the remarkably ventral position of the more ventral lateral line root—the superficial ophthalmic root—which has its exit directly below the VIII. The intra-medullary course of this root should be investigated. Its extremely ventral exit would appear to offer difficulties to its having a common internal center with the other lateral line roots. It is also interesting to note that while here it is the most dorsal of the preauditory lateral line roots which composes the buccalis; in Elasmobranchs, judging from Ewart's figures it is the more ventral root which goes over into this nerve.

Cole contributes also an interesting discussion of the homology of the chorda tympani. He upholds the view that the representative of the chorda in fishes is the pre-spiracular branch of the VIIth. While admitting that the nerve described by Strong in Amphibia as the mandibularis internus and homologized with the chorda is the chorda tympani, he denies its homology with the mandibularis internus of cartilaginous fishes, which is a post-spiracular nerve. Cole makes a careful examination of the morphological characteristics of the chorda in mammals and adduces reasons of weight in favor of his view. These cannot all be summarized here but consist partly in the relation of the branch in question to the mandibular arch, in the fact that it is composed principally of splanchnic sensory fibers while the post-branchials are principally splanchnic motor and in the inherent probability that so



important a division of a branchial nerve as the pre-branchial would be represented in the higher forms.

Such are some of the principal results of this sound research upon an important form. It is to be hoped that its author will extend his researches, as he intimates, to a study of the microscopic structure of the nervous system of *Chimæra*.  
O. S. S.

### The Trigemino-facial Complex of Fishes.<sup>1</sup>

This is one of several papers that have appeared during the past year, aiming at the complete homologization of the cranial nerve roots among the Ichthyopsida (and with higher forms). The primary purpose of the author was a comparison of the cranial nerve components of Teleosts as determined by Mayser (1881) with those recognized by himself in the Ganoid *Acipenser* in 1888.

The facts of homologization are essentially those determined independently by the other workers in this field (Strong, Herrick, Kingsbury); the interpretations, however, differ in many important points from those of the others, due apparently to a lack of comparison with other (higher) forms and a sufficient appreciation of the functional distribution of the components. As representing the teleosts were chosen *Esox* and especially *Lota*.

By a reexamination of the cranial nerve roots of *Acipenser* and the encephalic centers connected therewith, our author substantiates his former statements and conclusions, to the effect that there are (at least) five pairs of segmental nerves connected with the oblongata, each having a ventral motor root (or roots) and dorsal sensory roots, i. e. (1) the Vagus, (2) Glossopharyngeus, (3) Facial, (4) Second Trigeminal, and (5) First Trigeminal. This view leads him to reject the "lateral motor root" theory as not consistent with the observed facts. Among the most important additions to his former observations on the internal connections of the cranial nerves discussed, is the recognition that his system  $\gamma$  is largely the ascending root of the Vth cranial nerve (Trigeminus). He also finds that the motor root of each nerve receives a portion of its fibers from the Posterior Longitudinal Fasciculus.

In the comparison of the oblongata of *Acipenser* with the oblongata of *Lota* and the Cyprinidae, which constitutes the second portion of the paper, most important is perhaps the recognition that the so-called geniculate root of the Trigemini in Teleosts is the homologue

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<sup>1</sup> GORONOWITSCH, DR. N. Der Trigemino-Facialis-Komplex von *Lota vulgaris*. *Festschr. Gegenbaur*, Vol. III, pp. 1-44, Pl. I and II. Leipzig, 1897.

of the sensory root of the Facial in *Acipenser*; that the "lobi faciales" in *Lota* from which the roots spring are directly continuous with the Lobi glossopharyngei and Lobi vagales; and that, therefore, the Tuberculum impar (Lobus trigemini) of the Cyprinidae is the homologue of the Lobi faciales. No structure which might be compared to the Lobus trigemini of *Acipenser* was found in the Teleosts. Geronowitsch found their homologue, however, "proximo-lateral of the cerebellar crest." The internal origins and connections of the nerve-roots in *Lota* are given in detail in comparison with the conditions found in *Acipenser*.

A third portion of the paper is devoted to the analysis of the roots composing the Trigemino-facial complex and to a discussion of their distribution; the following points may be mentioned. *Ramus ophthalmicus superficialis* he finds to be derived from his Trigemini II; *R. ophthalmicus profundus* from Trigemini I. In the composition of the Hyo-mandibular it is found that, whereas in Ganoids it contains fibers from the facial and Trigemini II, in Teleosts it also receives fibers from Trigemini I. This fact he would explain on the supposition that the suspensory apparatus has been pushed forward into the territory innervated by the Trigemini I, for which view some comparative evidence is introduced. This has also, he believes, influenced the morphology of the Teleostean oblongata,—a suggestive thought.

The Palatine nerve is derived from the facial and is thought to be the homologue of the *Nervus rostri interni Acipenser*. The palatine nerve of *Acipenser* he believes to be represented by the *N. maxillaris inferior* in *Lota* which, therefore, equals the fusion of two distinct nerves in *Acipenser*.

This paper gives a helpful basis in facts for future comparative work on the cranial nerves, although, it is felt, its value would have been greatly enhanced had an analysis on the basis of function been more closely held in view. His segmental classification is open to criticism on many grounds. Sufficient evidence is not furnished of the ventral root of his Trigemini II, whereas there is evidence that it is sensory.

B. F. K.

### The Vagus Nerve of Teleosts.<sup>1</sup>

This paper, especially when considered in connection with the preceding, impresses upon the reader the need of comparative work on the cranial nerves of fishes; and also serves to illustrate the difficulties and dangers attending the consideration of one of the cranial nerves

<sup>1</sup> HALLER, DR. B. Der Ursprung der Vagusgruppe bei den Teleostiern. *Festchr. f. Gegenbaur*. Vol. III, pp. 47-101, Pl. I-IV. Leipzig, 1897.

apart from the others; which, in this case, are inadequately referred to, and sometimes incorrectly interpreted.

In the forty-four pages which the article covers, are set forth the results of a minute investigation of the internal origin of the vagus in *Salmo*, in connection also with specimens of *Perca*, *Leuciscus*, *Squalius*, *Barbus* and *Cyprinus*.

Three centers of origin and termination for vagal fibers are recognized,—a dorsal sensory nucleus, middle motor and ventral motor nucleus. The dorsal (sensory) nucleus, which is the direct continuation of the dorsal cornua of the spinal cord, is composed of two portions, an inner [Lobus Vagi autor.] and an outer; from these the vagal fibers are derived, springing in part from nerve cells located in the nuclei, from the diffuse nervous reticulum, and also sometimes from what he terms the “latero-dorsal longitudinal bundle” which he recognizes later as the homologue of the ascending root of the Trigemini in Cyprinoids (Mayser) [and it may be added in other Teleosts.]

The fibers derived from the middle nucleus are motor. The nucleus is of varying extent in the different forms and is regarded by the author as a differentiation of the part of the ventral horn lying nearest the central canal. The lower (ventral) nucleus is the direct continuation of the ventral horn and its cells are conspicuously larger. Fibers also of crossed origin occur from both the middle and ventral nuclei.

Dr. Haller adds a comparison with the Cyprinidae which possess a much concentrated oblongata; and, by means of literature, with higher forms (Batrachia, Reptiles, Birds, Mammals.)

In Mammals the Nucleus ambiguus is regarded as representing (in part) the middle vagal nucleus of fishes which also includes the homologue of the nucleus of the Hypoglossal nerve which, therefore, he regards as included in the vagus of fishes and not in the post-vagal nerves, which are discussed in the beginning of the article with conclusions to this effect. The homology of the fasciculus solitarius of mammals with the “latero-posterior longitudinal bundle” [ascending root of the Vth] is suggested, based on the connection with the dorsal cornua of the spinal cord and its relation to the vagus.

B. F. K.

#### The Ampullae of Lorenzini.<sup>1</sup>

This paper, upon the Ampullae of Lorenzini, is a preliminary publication of a portion of the results of a more extended study of the

<sup>1</sup> PEABODY, J. E. The Ampullae of Lorenzini of the Selachii. *Zoological Bulletin*, Vol. I, No. 4, pp. 163-177, 1897, 8 figs. in text.

lateral line system, Ampullae of Lorenzini and vesicles of Savi of Selachians. The structure of these interesting organs is investigated to determine the mode of nerve termination and gain evidence as to their function,—secretory or sensory.

The Ampullae are discussed from the standpoint of their grouping, gross anatomy, histology, innervation and physiology. The inner end of each ampullary tube, the Ampulla proper, of which there are some fourteen to fifteen hundred in *Galeus*, possesses lateral pockets varying in number from 6 to 12; the nerve enters the base of the ampulla which is involuted forming a central column (the centrum) from which radiate the partitions between the pockets. No special sensory epithelium was found; the ampullary tube itself is lined by a single layer of rather flattened cells which also cover the upper surface of the centrum cap. The walls of the pockets possess two layers of cells, a surface layer and a deeper layer of short columnar cells. The innervation of the ampulla can best be stated in the author's own words,—“Five to seven medullated fibers coming from the (seventh pair of) cranial nerves enter each ampulla from below and pass up the centrum. Just beneath the centrum cap the sheath disappears. The axis cylinders, continuing on their course, send out lateral branches, which after division and ramification beneath the centrum cap run out along the partitions to the outer walls of the compartments. Here minute fibrils play over the bases of the deeper layer of cells, ending in slight enlargements on their surfaces.” (p 174.)

The methylene blue method of intra-vitam staining was employed, modified to suit the kind and nature of the tissue.

Of the two possible functions, sensation or secretion, the former is believed to be far the more plausible. In its support are arrayed the rich nerve supply and the greater number and complexity in more active Selachians than in those less active (Torpedo)—a correlation found also in the lateral line system.

The system is most puzzling, both as to its morphological significance and its function—sensory though it be—and further work, especially bearing on the nerve supply in relation to that of the lateral line system will be very welcome; as also the results of experimental work upon the function of the system, which the author has in progress.

B. F. K.

### The Brain of the Sturgeon.

J. B. Johnston, in the *Zoological Bulletin*, I, 5, describes the histology of the olfactory tubers, the fore-brain and the habenular tracts in *Acipenser* as made out by the Golgi method. In the olfactory tuber he



finds six kinds of cells aside from the specific or mitral cells. The granule cells have axis cylinders and dendrites and are therefore nerve cells. There are also cells similar to the so-called cells of Cajal. Associational cells with short axis cylinders are present in the glomerular zone. The large mitral cells are provided with non-glomerular dendrites. In the dorso-median region of the fore-brain there is a large incompletely differentiated nucleus of cells with short axis cylinders constituting an imperfect epistriatum. A group of cells on the lateral surface of the fore brain agrees in position and apparently in connection with the cortex lateralis of Reptilia. The cortical region of the fore-brain is connected with the ganglion habenulae by a tractus cortico-habenularis and there is also a tractus olfacto-habenularis. Meynert's bundles do not end in the interpeduncular, but undergo partial decussation there and pass on towards the medulla.

C. L. H.

#### The Cerebellum of Fishes.<sup>1</sup>

After a brief description of the cerebellum of low types of Selachians the author institutes comparisons with the same organ in the ganoids and teleosts, chiefly as described by other writers. The result of the comparison is to lead the author to the conclusion that the cerebellum of the selachians is composed of two portions, the cephalic of which is homologous with the valvula,<sup>1</sup> the other portion is strictly homologous with the cerebellum of teleosts. The decussation of the trochlearis is thus still retained as the cephalic boundary of the cerebellum. In general the very obvious suggestion of Strong, the Herricks and others that the differentiation of the regions of the medulla oblongata is largely influenced by the peripheral nervous distribution is again made emphatic.

C. L. H.

#### The Development of the Retina According to Cajal.

Professor R. Greef, who translated Ramon y Cajal's monograph on the retina has given a full resume of the recent studies by the same author as published in full in the *Journ. de l'Anat. et de la Phys.*, Sept., 1896.

The rods and cones arise as very similar unipolar cells attached by stalks to the outer limiting membrane. Prior to this stage the visual

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<sup>1</sup> RUD. BURCKHARDT. Beitrag zur Morphologie des Kleinhirns der Fische. *Arch. f. Anat. u. Phys.* 1897.

<sup>2</sup> This organ the author still calls the *valvula cerebelli* in spite of the false homology involved.

elements are round protoblasts in process of proliferation. The unipolar stage is followed by a bipolar stage in which a process is formed that extends to a variable distance toward deeper parts of the retina. Cajal regards the visual cells as different in kind from the neuroglia as well as the true nerve cells for, as is claimed, in these cells the cellipetal and not cellifugal process is first to develop. (A different interpretation than this seems possible.) The so-called horizontal cells proved unamenable to the silver method but two types were distinguished, one with fine and the other with coarse axis cylinders. Two distinct sorts of bipolar cells, one for the rods and the other for the cones are distinguished. The second part of the paper is devoted to the structure of the retina of birds. The so-called association spongioblasts are supposed to be connected with the centrifugal fibers whose existence is regarded as proven. The principal type of ending, the pericellular nest, is very like that of the so-called basket cell of the cerebellum. Cajal still maintains as against Dogiel that anastomoses of nerve fibers do not occur in the retina, and ascribes the evidence to the contrary to imperfect observation.

C. L. H.

## PHYSIOLOGY.

### The Function of the Protoplasmic Processes of Nerve Cells.<sup>1</sup>

This article throws new light upon the function of the protoplasmic processes of nerve-cells, a problem which neurologists have been investigating ever since Golgi announced that there was a structural difference between these processes and the axis-cylinder prolongation of a nerve cell.

The first part of the paper is a historical résumé of the growth of opinion on the subject. Among other things, the author makes the following statements. Golgi still holds that the function of the dendrites is purely nutritive. Although several early investigators thought they had demonstrated the truth of his hypothesis, yet recent investigators do not hold this extreme view. Ramon y Cajal and Van Gehuchten hold that both the ramifications and the distribution of the dendrites fit them for the reception and communication of nervous impulses and that that is undoubtedly their function. Lenhossèk holds a similar but not quite so exclusive view. Kölliker holds that our present technique does not yield an answer to the problem.

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<sup>1</sup> SEMI MEYER. Ueber die Function der Protoplasmafortsätze der Nervenzellen. *Berichte über die Verhandlungen der Königlich Sächsischen Gesellschaft der Wissenschaften zu Leipzig*. 1897, V, VI, pp. 475-496, Taf. I, II.

In the remainder of the paper the author discusses the result of his recent researches upon the nervous systems of young Guinea pigs, young rabbits and adult rabbits. The brains of about one hundred animals were studied by his (Meyer's) intra-vitam methylene blue method. Dr. Meyer claims that this method of studying the relation of nerve cells to nerve fibers is superior to Golgi's. The plates illustrating this article support this view.

The author's sections showed conclusively: (1) The protoplasmic cell-process or dendrites and the cell-body are structurally similar. (2) The axis-cylinder first comes in contact with the cell at the apex of a dendrite. (3) The axis-cylinder process splits into numerous branches which ramify over the surface of the cell and its dendrites, enveloping them in a basket of fibrils. (4) In some cases the axis-cylinder process begins to split on the dendrite with which it first comes in contact; in others the splitting does not begin until the cell-body is reached. (5) In adult brains, the cell-enveloping fibrils are more numerous and closer together than they are in younger brains. (6) Whether these cell-enveloping fibrils anastomose or not is uncertain; but none of the sections showed any trace of anastomosis.

Although the existence of the cell-enveloping fibrils could not be demonstrated in all parts of the brain, yet they were found in so many places that the author thinks improved technique will show that they are present throughout the nervous system. The author thinks there is an intimate union of the tips of the enveloping fibrils with substance of the nerve cells.

These discoveries led to the following conclusion: Since there is no structural difference between dendrites and the body of the nerve cell, there is no physiological difference between them. The function of a dendrite is nervous.

C. H. TURNER.

### **Junction of Vagus with Superior Cervical Ganglion.<sup>1</sup>**

In two cats the central end of the vagus, cut a little below the larynx, was turned forward and joined to the peripheral end of the cervical sympathetic. The object of the experiments was to see whether the vagus nerve fibers are capable of forming connections with any of the structures with which the spinal nerve fibers of the cervical sympathetic are normally connected. The experiments permit a decisive affirmative answer: "efferent fibers of the vagus had either grown along

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<sup>1</sup> Note on the Experimental Junction of the Vagus Nerve with the Cells of the Superior Cervical Ganglion. By J. N. Langley. *Proc. Roy. Soc., LXII*, No. 384, 7 Feb., 1898.

the peripheral end of the cervical sympathetic, and formed nerve endings around the cells of the superior cervical ganglion, or they had united directly with the sympathetic fibers. That the former had taken place I infer from the fact that the regenerated nerve contained medullated fibers larger than those proper to the sympathetic.

"I conclude from the experiments that there is no essential difference between the efferent 'visceral' or 'involuntary' nerve fibers, whether they leave the central nervous system by way of the cranial nerves, by way of the sacral nerves, or by way of the spinal nerves to the sympathetic system. All of these fibers I take to be pre-ganglionic fibers. And I think that any pre-ganglionic fiber is capable, in proper conditions, of becoming connected with any nerve cell with which a pre-ganglionic fiber is normally connected; although apparently this connection does not take place with equal readiness in all cases. On the whole it appears to me that the functions exercised both by pre-ganglionic and by post-ganglionic fibers depend less upon physiological differences than upon the connections which they have an opportunity of making during the development of the nervous system and of the other tissues of the body."

Some earlier experiments upon the cervical sympathetic are reported by Dr. Langley in the *Journal of Physiology*, Vol. XVIII, 1895, p. 280 and Vol. XXII, 1897, p. 215. Among other interesting conclusions, it appears from these operations that during regeneration sympathetic fibers sometimes effect connections other than the normal, so that the functions of the regenerated fibers may differ in minor features from those exhibited before the operation.

These facts have a morphological, as well as a physiological, interest. It seems to the reviewer very probable on purely morphological grounds that the chief vagus nucleus (lobus vagi of fishes) contains the cranial representative in all vertebrates of the lateral horn zone of the spinal cord; and the fact that the former can by experiment be functionally substituted for the latter seems to bear out this idea.

C. J. H.

### Degenerative Changes after Resection of the Vagus.<sup>1</sup>

A good historical review of the problems especially under investigation precedes the account of the experiments undertaken. The vagus

<sup>1</sup> Zur Frage über Veränderungen im Nervensystem und in inneren Organen nach der Resection des N. vagus und des N. splanchnicus. By Dr. W. NIEDZVIETZKY. *Bull. soc. imp. des Naturalistes de Moscou*, Année 1896, No. 3, 1897, p. 515.



was resected in four adult rabbits. In the central nervous system the sensory vagus nucleus was reduced in size along its entire length. This nucleus is divided into two parts. The inner, of large often bipolar cells, almost completely disappeared on the operated side; the outer, more dorsal, portion, of smaller cells, was less affected. The motor vagus nucleus, N. ambiguus, was greatly atrophied upon the operated side and less so on the opposite side. The funiculus solitarius in its caudal portion was reduced upon the operated side, i. e. those fibers which it receives from the vagus were degenerate. These comprise from one third to one half of the total number of fibers in this bundle, the remainder being derived from the IX nerve. The funiculus gracilis is a little reduced on the operated side. The arcuate fibers toward the raphe are reduced in the operated side.

An interesting morphological point is the demonstration of a commissure containing medullated fibers between the lower or caudal ends of the two funiculi solitarii. This is strictly comparable with the commissure in the commissural nucleus found in the mouse by the Golgi method in the hands of Cajal. (See notice, this Journal, Vol. VII, p. xxiii.) A similar commissure is found in the birds by Koch and the reviewer believes that such fibers are also represented in the commissura infima Halleri of the fishes.

A section is devoted to the alterations in the other organs of the body in the cases mentioned above, and a final section to the results of the resection below the diaphragm of the N. splanchnicus major in two adult dogs. The dogs were killed 16 and 21 days respectively after the operation. The nerve, the sympathetic ganglion from which it springs and various parts of the cervical spinal cord corresponding to the places where rami communicantes go off to this sympathetic ganglion were examined. No alteration was found in any of these except in the sympathetic ganglion, where there was vacuolation of the nerve cells. The author concludes that this nerve is a motor nerve, whose cells of origin are wholly in this sympathetic ganglion.

C. J. H.

#### **Secondary Changes in the Primary Optic Centres in Case of Bulbus Atrophy.**

In this paper,<sup>1</sup> O. v. Leonowa offers details of a number of cases of congenital anophthalmia and atrophy in young children which may be sought in the original.

The following points may be noted as expressing the more important general results: In the optic nerve there are two distinct classes of

<sup>1</sup> *Arch. f. Psychiatrie*, XXVIII, I.

fibers, the one being coarse, the other fine. The finer fibers not only enter the cephalic bigemina but also are distributed to the geniculata externa. The greater part of the optic nerve fibers arise in the ganglion cells of the retina and are distributed to the geniculata externa in the form of terminal arborizations. Other fibers arise in the bigeminum and send their fibrous end-arborizations to the retina. The course of the fibers which arise in the geniculata and pulvinar and are supposed to pass to the occipital lobe, the author has been unable to trace. It is suggested that the conditions for nervous transference and coordination are afforded by the cells of Golgi's second order. The fact that the eye-muscle nerves are intact is explained as a corollary of the law that the nerves are developed in connection with the muscles (which still remain in these cases) though the author's earlier studies seem to show that the muscular system may be well developed in the absence of the nervous system.

As stated in earlier papers by the same author, the fourth layer of the occipital region of the cortex is absent in anophthalmic cases and a high significance for the act of vision is accordingly attributed to them. These cells may have something to do with the accommodation reflexes.

C. L. H.

#### **On the Alleged Atrophy of the Nasal Epithelium after Section of the Olfactory Nerve.**

Dr. Julius Neuberger, in a paper in the *Centralblatt für Physiologie*, Oct. 30, 1897, entitled "Ueber das Verhalten der Riechschleimhaut nach Durchschneidung des Nervus olfactorius,"<sup>1</sup> presents an epitome of the conflicting results of the work of previous investigators on this subject, and in relation to these, the conclusions to which he has arrived in his own researches. Eckhardt and Ecker simultaneously distinguished for the first time the true olfactory, from the ordinary epithelium cells in the mucous membrane of the nose, and simply assumed the connection of the olfactory fibers with the former type of cells. Later Max Schultze figured diagrammatically the probable connection of such a fiber with such a cell, though it could not be demonstrated by actual observation. In spite of the fact that Kölliker (in 1856) pronounced it an "histological impossibility," this view gradually won recognition until it has become the commonly accepted opinion. New methods of research (vital methylene blue and Golgi), applied by Ehrlich, Ramon y Cajal, Grassi and Castrouovo, van Gehuchten, and

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<sup>1</sup> Aus dem anatomisch-biologischen Institute der Universität Berlin. Director: Prof. O. Hertwig.

others, abundantly confirmed Max Schultze's theoretical condition. Previous workers had, however, attacked the problem experimentally. C. K. Hoffmann operated on frogs and mammals finding, as resulting therefrom, what appeared to him to be a fatty degeneration of the peripheral nerve and of the cells of the nasal epithelium. These results, however, in the opinion of Neuberger, will not permit of close scrutiny, and, moreover, have been rendered of doubtful value by the counter-researches of Schiff on young dogs and Colasanti on frogs, neither of whom found any such degenerative change. So again, Exner and Lustig thought they had found an atrophy, as well as the entire loss of cilia, as the result of similar extirpation in frogs (they failed completely in the same with rabbits); but these conclusions also seem to be not well substantiated because of faulty observation. The work of B. Baginsky on rabbits was supposed to have been conclusive since he made sections through the entire membrane; but his observations are rendered untrustworthy by his own admission of important collateral injuries in performing the extirpation. In view of these contradictory conclusions arrived at by so many different investigators, Neuberger, at the suggestion of Dr. R. Krause, decided to study the duck, an exceptionally good subject for the extirpation because of the long *fila olfactoria*. He employed every means to avoid the mistakes of previous researches, using a variety of methods and subjects. The results of his investigations, taken in connection with the work of Schiff and Colasanti, serve to confute the conclusions of the other investigators to whom reference has been made. In concluding, he summarizes by saying that the cross-section of the olfactory nerve in the duck results in a quite noticeable atrophy caudad of the point of operation in the corresponding brain centre, but that the olfactory mucous membrane in both the duck and the frog exhibits no alteration resulting therefrom. This conclusion furnishes, he says, a new link in the chain of evidence for the new conception of the morphology of the nasal epithelium, *viz.* that the olfactory cells really are nothing more nor less than modified ganglion cells lying in the peripheral epithelium, which is thus the real originating centre of the olfactory tract. This view is important in that it contradicts the prevailing opinion that the olfactory nerve differs fundamentally from the other cranial nerves, and in throwing additional light on the newer view, advocated also by the editor of this journal, that it simply exhibits an arrested stage of development which is the primitive condition of every sensory nerve, and thus is of fundamental importance in understanding the formation of central neural connections. The directions given for the proper man-

ner of executing the extirpation on the duck, and the preparation of the material for microscopical examination, are worthy of note. The studies on frogs were used as checks on the results obtained from the ducks, and resulted in every case in confirmation only. A bibliography is appended

H. HEATH BAWDEN.

### Relations Between the Nose and Sexual Organs.<sup>1</sup>

While the relation between sexual disturbances and morbid conditions of the eye, ear and throat was early recognized, the part which they play in the production of nasal disease has until very recent times been overlooked. The earlier physiognomists, indeed, laid great stress on the size and form of the nose as an indication of corresponding sexual qualities, while in astrology Venus presided over the nose as well as over generation. But until quite recently it has not received the attention it deserves from either the medical profession or from investigators. Dr. Mackenzie has already pointed out, in a previous publication (*On Nasal Cough and the Existence of a Sensitive Reflex Area in the Nose*, *Am. Jour. Med. Sciences*, July, 1883) the existence of a definite well-defined sensitive area, whose stimulation, either through a local pathological process, or through the action of an irritant introduced from without, is capable of producing an excitation which finds its expression in a reflex act or in a series of reflected phenomena. This tissue is essentially the anatomical analogue of the erectile tissue of the penis. It is the temporary erection of this tissue, the dilation of its cells being, in all probability, under the direct dominion of vasomotor nerves derived through the sphenopalatine ganglion, that constitutes the anatomical explanation of the stoppage of the nostrils in coryza and allied conditions. This erectile area is, moreover, especially concerned in the evolution of the many curious "reflex" phenomena which are observed in connection with nasal affections. Indeed, the changes which it undergoes seem to lie at the foundation of nasal pathology, and furnish the key not only to the correct interpretation of nasal disease, but also to many obscure affections in other and remote organs of the body. That an intimate physiological relationship exists between the sexual apparatus and the nose, and especially the intra-nasal erectile tissue, is supported by the following physiological data corroborated by evidence from pathology. These are

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<sup>1</sup> The Physiological and Pathological Relations Between the Nose and the Sexual Apparatus of Man. By J. N. Mackenzie, *Johns Hopkins Hospital Report*, Jan., 1898, pp. 10-17; and *Alienist and Neurologist*, XIX, 2, April, 1898.



summarized as nearly as possible in Professor Mackenzie's own words :

(1) In a certain proportion of women whose nasal organs are healthy, engorgement of the nasal cavernous tissue occurs with unvarying regularity during the menstrual epoch, the swelling of the membrane subsiding with the cessation of the catamenial flow. Pathology also furnishes a variety of cases of analogous nature. The investigations of Fliess would seem to indicate that painful, profuse and irregular menstruation may be temporarily dissipated by the application of cocaine to the nasal mucous membrane, or permanently controlled by cauterization. According to him, only the inferior turbinated body and the tuberculum septi possess a special relation to the dysmenorrhœic pains. These two localities he accordingly designates as genital zones (*Genitalstellen*).

(2) The presence of vicarious nasal menstruation.

(3) The well-known sympathy between the erectile portions of the generative tract and other erectile structures of the body, e. g., the nipples.

(4) The occasional dependence of phenomena referable to the nose during sexual excitement, e. g., sternutation, epistaxis, occlusion of the nasal passages.

(5) The occasional dependence of genito-urinary irritation upon affections of the nasal passages.

(6) Venery and masturbation seems to have a tendency to initiate inflammation of the nasal mucous membrane, or to aggravate existing disease of that structure.

(7) It is, finally, quite possible that irritation and congestion of the nasal mucous membrane precede, or are the excitants of, the olfactory impression that forms the connecting link between the sense of smell and erethism of the reproductive organs exhibited in the lower animals and in those individuals whose amorous propensities are aroused by certain odors that emanate from the person of the opposite sex.

H. HEATH BAWDEN.

## PSYCHOLOGY.

### **Absolute Sensitiveness of Various Parts of the Retina When the Eye is Accommodated for Darkness.**

Under the above topic J. v. Kries contributes a suggestive article to the *Zeitschrift f. Psychologie u. Physiologie d. Sinnesorgane*. XV, 5-6.

It is well known that the fovea possesses less absolute sensitiveness to light than excentric portions of the retina although the latter is the

spot of clearest vision. This is especially true of the eye when accommodated to darkness.

The first set of experiments with a mixed (blue) light were so conducted that a small disk was placed on a black background and faintly illuminated, after which it was moved in a lateral direction till a point was found where it was no longer visible. The sensitiveness was determined in terms of the threshold value of the fovea. For about two degrees at the center the sensitiveness was found to be nearly constant, beyond which distance it increased rapidly to beyond five degrees—most rapidly on the nasal side of the retina.

The second set of experiments shows that red light is an exception as its effect diminishes from the fovea while the increase is more marked in the case of blue than of yellow light. The author suggests that as the red light does not affect the rods while other colors do, and the rods are more numerous toward the periphery, the increase in one class of colors is to be ascribed to their superior efficiency on the rods and the rate of increase will depend on the "rod-valence."

For numerous interesting details see the original. C. L. H.

### **The Psychology of Invention.<sup>1</sup>**

The paper by Professor Royce under the above caption is accessible to most of our readers but a summary of the conclusions and of the methods suggested for investigation may interest those who are not psychologists by profession.

It is stated that "important inventions do not occur, in general, except under particular social conditions", and the individual varies more when variation is encouraged, when independence, private enterprise, is favored by social environments. Accordingly, children in the country or isolated from school routine often show greater inventiveness in their games than do children early submitted to the routine of large schools. In history also periods of great individualism have been periods of great inventiveness, as during the Renaissance and Revolutionary period. Professor Royce has endeavored to produce in an experimental way conditions which in a small way should simulate those which form the basis for the reaction between the subject and the environments tending to originality.

The experiments consisted in requiring the unbiased subjects to draw a series of designs which should not imitate anything; at first hastily, and then deliberately. Then the same subjects were requested

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<sup>1</sup> Psych. Rev. V, 2. March, 1898.

to draw designs as unlike as possible to diagrams exhibited to them. The first series showed that the diagrams betrayed sub-conscious habits. (One of the records, we venture to believe, was based on embroidery or needle-work experience.) Three distinct kinds of results are produced by the intruding stimulus. (1) In some it produces a tendency to vary. (2) Others are made more critical and cautious. (3) In many cases the result is a blending of the new with the old and may involve true invention. The same laws are detected in the broader social sphere.

C. L. H.

### **Projection of the Retinal Image.**

In the American Journal of Psychology for October, 1897, Dr Pillsbury calls attention to a simple but on the whole very convincing observation indicating the truth of the empiristic explanation of localization. The observation is one that all microscopists can confirm, i. e., that, in using the Abbe camera lucida, the image of the object is usually seen, not in direct line, that is, in the field of the microscope, but in the refracted direction or upon the drawing board. The eye is, in this case, offered the choice between two possible lines of reference and selects, not as would be expected, on a nativistic theory, the perpendicular, but a line in which the dynamic (muscular) element is the determinant. The direction of the ray which produces the impression is then comparatively unimportant in determining the place to which we attribute to the origin of the stimulation. (Compare review in the last number of this Journal of the article by Professor Stratton on "Inversion of the Retinal Image.")

C. L. H.

### **Color Mixing in the Eye.<sup>1</sup>**

The above is the continuation of the paper entitled *Farbeninduction* which appeared in the same periodical for 1895. The paper is too technical to be reviewed in detail in our pages and we must be content with the reproduction of the author's summary of his own conclusions. He has succeeded in so arranging the experiments as to make apparent the blue dispersion observed by Helmholtz in daylight. The most refrangible rays have a much lower "threshold both for light excitement and color reaction than the less refrangible rays. Blue-violet, accordingly, soon reaches its maximum saturation and maximum luminousness. In general, then "When mixed with black as well as in case of any other method of reduction of the energy the right side of the spec-

<sup>1</sup> *Untersuchung zur Farbenmischung im Auge*. K. B. Aars. Videnskabselskabets Skrifter, 1897. No. 8.

trum gains in relative color value while, in case of admixture with white or any other method of increasing the energy, the left portion of the spectrum increases in relative color value. C. L. H.

### The Emotional Content of Dreams.<sup>1</sup>

The author arrives at practically the same result as that reached by the writer of these lines, namely that the essential content in dreams is not the intellectual but the feeling element. He says "Our human grief and joy root in action and the drama of life and this canon we apply to the interpretation of our dreams." The truth of this interpretation he calls in question and very justly, for, as he says, the physiological facts are directly hostile to the hypothesis of a rich ideational content. The dream, he concludes, "consists of a succession of intense states of feeling supported by a minimum of ideational content." "The feeling is primary; the idea-content is the inferred thing." The present writer, in the course of a study of dreams extending over a series of months, arrived at the same conclusion as the result of the constant experience that the dreams, when recorded with closed eyes before the blood currents were accelerated by a change of position were found quite or nearly devoid of intellectual content, while those taken after rising had a garb of intellectual interpretation which was generally congruous in proportion to the time that had elapsed since awakening.<sup>2</sup> An interesting report of the subjective experiences during recovery from the effects of nitrous oxide in the same number of the Review adds confirmation to this hypothesis.

C. L. H.

### TECHNIQUE.

#### Experiments with the Weigert Methods.<sup>3</sup>

The experiments detailed in this paper were conducted in connection with a research now in progress at the Pathological Institute of the New York Commission in Lunacy and, as these data, so far as they have any permanent value, will be of especial interest to comparative

<sup>1</sup> ROBERT MACDOUGALL. The Intellectual Content in Dream Consciousness. *Psychol. Review*, V. 2.

<sup>2</sup>Cf. *Journ. Comp. Neurology*, Vol. III, p. 17, 1893.

<sup>3</sup>Report upon a Series of Experiments with the Weigert Methods, with Special Reference for use in Lower Brain Morphology. By C. JUDSON HER-  
RICK, Associate in Comparative Neurology, Pathological Institute of the New  
York State Hospitals; Professor of Zoology, Denison University. Utica,  
N. Y., State Hospitals Bulletin, October, 1897. Issued May, 1898.



neurologists, a portion of them are here repeated. The introductory and concluding sections are given nearly entire and the summaries of the others. Only the more important of the experiments which gave positive results are reprinted, but those which are given are numbered as in the original paper.

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The writer has been engaged for several months upon an investigation, which is still incomplete, of the components of the cranial nerves of the bony fishes. This research has involved the reconstruction from serial sections of the entire courses of the cranial nerves from their nuclei of origin or termination in the brain to their peripheral termini. Upon plots of the cranial nerves, as thus reconstructed, the components of each nerve have been entered, each component having been followed, so far as possible, through the entire course of the nerve from central origin to peripheral end-organ.

Proximally the components are for the most part easily recognized from the nuclei of the brain with which they are related; peripherally the several components of a nerve trunk are again analyzed as they diverge toward their respective end-organs; but in their intervening courses the fibers of the several components are so intimately intertwined that analysis would in most cases be impossible were it not for the fact that the several classes of fibers exhibit well-marked and tolerably constant differences in their size and the character of their myelination. The fiber-characters of each component are surprisingly similar in all groups of lower vertebrates which have thus far been examined, and the human nerves will, I think, be found also to conform, judging from the rather meager data now available.

It was in the search for methods adequate for this investigation that the experiments described below were undertaken, and this will explain the rather narrow limits between which the experiments were confined and in particular why certain procedures favorable for serial section cutting, such as paraffin embedding, were uniformly adhered to. The technical requirements of the case were indeed rather exacting, for in order to secure Weigert preparations adapted to the purpose we must have, first, absolutely perfect fixation of the medullary nerve sheaths, far more perfect than is ordinarily given in bichromate of potash preparations. Second, perfectly continuous serial sections must be made through the entire head of the animal under investigation; for this purpose ribbon cutting after paraffin embedding offers very obvious advantages over the celloidin method. Third, the specimens, though small, should be adult or nearly so, in order that the medullary sheaths

of the nerves may be fully laid down. This point, though not absolutely necessary, is certainly a great advantage. The last condition involves, fourth, quite rigorous decalcification in any bony fish. And this is perhaps the point of chief difficulty, for not only must the tissues, especially the medullated nerves, be well preserved during the process of decalcification, but they must be left in such a chemical condition as to be amenable to the Weigert reaction subsequently. Finally, one has to determine experimentally the particular combination of mordant, stain and decolorizer which will give the clearest results.

The chemistry of the Weigert reactions has not, to my knowledge, been sufficiently worked out to make it possible to predict in advance of actual trial the result of any given combination of fixer, mordant, stain and decolorizer; it is in the hope of sparing some other investigator the weary drudgery of similar blind experimenting that the results of several of my experiments are here published, though the number of failures far exceeds that of successful preparations. It is hoped, too, that these data may be of value in understanding the nature of the Weigert reaction and allied processes.

The same general method of procedure, which has in my hands in some cases given most excellent preparations, has been adhered to throughout the series of experiments, and is to be understood as applying to each case unless otherwise stated. This procedure involves the fixation and decalcification of the specimen entire or nearly so, in large specimens one side of the head being sliced off with a sharp knife and scissors so as to open thoroughly the cranial cavity without injury to the structures in the median line. The specimen is then dehydrated in alcohols, cleared in cedar oil, embedded in paraffin and cut into serial sections by means of a Minot microtome. Cedar oil is preferred to the other clearing oils because, during the long sojourn which is sometimes necessary, its effect is less injurious than that of any other clearing agent. Previous to the embedding or during that process the specimens should be aspirated with a two-way syringe or under the receiver of a good air pump to remove from the cavities of the body the gases evolved during decalcification. If the aspiration is conducted during the stay in cedar oil, the exhaustion should be carried on until the pressure is measured by five to eight mm. of mercury and the specimen held at this pressure for several minutes. By this process large specimens can be permeated as thoroughly with paraffin as with celloidin, though of course the times in all of the solutions, especially in the paraffin bath, must be considerably prolonged. The ribbons may be mounted on the

glass slips by means of Mayer's albumen, first flattening them out on warm water if necessary to remove all wrinkles, and after passing out of the absolute alcohol it is well to flow over each slide a very thin solution of celloidin, draining quickly and allowing to set for a moment before passing down into the lower grades of alcohol. The celloidin film will prevent the loosening of the sections in the staining fluid, which will sometimes occur with any other mode of fixing the sections to the slide, and will in no way interfere with subsequent manipulations, except slightly to retard them. If a thicker film is used the previous use of the albumen may be dispensed with and the film bearing the sections may be cut off from the slide and carried through the subsequent manipulations whole just like an ordinary celloidin section, though for serial section work I much prefer to keep the sections fixed to the slide on which they are to be permanently mounted. With the thin celloidin film the final dehydration should be done in origanum or carbol-xylol, though if the sections are thin I have not usually experienced any difficulty in dehydrating in absolute alcohol, as the stay in the strong alcohol can be so shortened as to remove the danger of the solution of the film. The sections are mordanted and stained on the slide in photographic trays or in staining tubes, the Coplin staining jar (Queen and Co.) being the best jar for the purpose; and in all of my experiments these processes were carried on at the ordinary summer temperature except where otherwise noted. Doubtless some of my results would have been different if the more usual celloidin embedding and mordanting in the block had been followed, and especially if the incubating stove had been employed during the process of mordanting; yet from my experience thus far in the matter I am inclined to think that these are factors of relatively slight importance and that more depends on the relations of chemical affinity within the tissues than upon accidents of temperature and other physical features of that sort, though there is no doubt regarding the value of mordanting and staining at blood heat to shorten the times of these processes.

For the composition of the fluids mentioned, when this is not given, the reader is referred to Bolles Lee's *Vade Mecum*.

In most cases the processes of fixation and decalcification were carried on together by means of the same fluid. First, the more usual decalcifiers, nitric acid, picric acid, etc., were tried in various combinations and these were afterwards replaced by acids which give a more faithful fixation. In the following summary the trials will be arranged first under the head of the fixing fluids, and under each of these the several mordants and stains. Only two kinds of fishes were employed



in these tests, *Menidia notata* and *Fundulus hereroclitus*, both small species, and the initial after the serial number in each case indicates which of the two species was employed in that test. All specimens were adult unless otherwise stated.

#### I.—FIXATION IN NITRIC ACID MIXTURES.

*Summary.*—None of the mixtures containing nitric acid, including several not mentioned above, gave a satisfactory fixation either of the medullary sheaths of the nerves or of the general tissues, and in most cases subsequent staining by the Weigert methods is impossible, either because the tissue will not take up the stain or because in decolorizing it bleaches uniformly.

#### II.—FIXATION IN PICRIC ACID MIXTURES.

- 11 *F.* A small specimen was treated for 8 days with,  
 Picric acid, saturated in water, 90 cc.  
 Acetic " (glacial), 1 cc.  
 Formalin, 10 cc.

For complete decalcification further experience shows that a longer time, at least two weeks, is necessary. Sections were mordanted for 45 minutes in a 4 per cent. solution of iron alum, stained in a  $\frac{1}{2}$  per cent. solution of hæmatoxylin in water for one hour and decolorized in 2 per cent. iron alum. The fixation is good and the axis cylinders are well differentiated. The medullary sheaths are, however, not well preserved and are stained scarcely at all.

14 *M.* The specimen was immersed for one month in the following mixture :

- Picric acid, saturated in water, 90 cc.  
 Iron alum, cryst., 4 g.  
 Formalin, 10 cc.

Decalcification was complete and the tissue very well preserved. But sections stained in  $\frac{1}{2}$  per cent. solution of hæmatoxylin in water for from 15 minutes to 5 hours and decolorized in 2 per cent. iron alum failed to differentiate the nerve sheaths properly. The whole tissue decolorized nearly uniformly. Other sections which were treated with Delafield's hæmatoxylin failed to take up any of the stain. Upon staining with Ranvier's picro-carmin the sections show excellent preservation of all the tissues, though the nerve sheaths are badly shrunken.

15 *M.* Sections from the same block as the last, mordanted for 16 hours in 5 per cent. potassium bichromate, stained for 6 hours in Weigert's hæmatoxylin and decolorized in Weigert's decolorizer did not differentiate the medullary sheaths and were in worse histological condition than in the previous case. The long soaking in aqueous solutions seems injurious, the nerve sheaths especially being more shrunken.

*Summary.*—Several other picric acid mixtures were tried, including two of vom Rath's formulæ; but in no case were the nerve sheaths properly preserved, nor did they give satisfactory Weigert stains. I



am satisfied, however, that both the picro-acetic formalin and the picro-iron-alum-formalin are very useful formulæ for general histological purposes, particularly where a slight decalcifying power is required. But the medullated nerves seem to be the tissues for which these mixtures are least adapted, and for the purposes of this research all picric acid combinations were discarded.

### III.—FIXATION IN CHROMIC ACID MIXTURES.

*Summary.*—Chromic acid, like nitric and picric acids, has a very injurious effect upon the nerve sheaths, even when applied in very dilute solutions and for a time far too short to permit of much decalcifying effect. Even in the presence of very strong formalin this injurious effect is still manifest. It is, moreover, in fishes, at least, not favorable for subsequent Weigert's staining.

### IV.—FIXATION IN ACETIC ACID MIXTURES.

*Summary.*—Acetic acid alone, like chromic acid, has a deleterious effect upon the nerve sheaths; and this effect is exerted even in the presence of formalin solutions sufficiently strong to fix the sheaths well if acting alone. Acetic acid in combination with sublimate has a still worse effect upon the medullated nerves, the white matter of the brain being more or less gelatinized. Other combinations of sublimate which I have tried lead me to condemn it (whatever may be its virtues for other purposes) as a poor fixer for nerve fibers.

### V.—FIXATION IN CHROM-ACETIC MIXTURES.

I have found Fol's chrom-acetic a most excellent fixing fluid, not only for general tissues, but especially for the brains of bony fishes. The medullary sheaths of the nerves are, however, less faithfully fixed than most of the other tissues. The addition of formalin to the mixture corrects this defect in a measure; the fluid has not, however, sufficient decalcifying power for the present purpose. The substitution of formalin for the osmic acid in Flemming's stronger formula gave much better results, as shown by the examples below.

24 F.	A small specimen (4 cm. long) was treated for seven days with	
	Chromic acid, 1 per cent.,	15 parts.
	Glacial acetic acid,	1 "
	Formalin,	4 "

The sections were mordanted in Wolter's fluid for 20 hours,		
	10 per cent. vanadium chloride,	2 parts.
	8 per cent. aluminium acetate,	8 "

They were stained for 24 hours in acid hæmatoxylin and differentiated with Weigert's decolorizer. This gives very excellent preparations. The fixa-

tion is good, though not so perfect as the osmic acid fixation to be mentioned beyond. The differentiation is good centrally, but not so brilliant peripherally as desired.

25 *F.* The same fixation, mordant and stain, but decolorized in Kultschitzky's fluid. About the same result as in the last case.

26 *F.* The same fixing fluid as in No. 24, applied 14 days, mordanted in 4 per cent. iron alum, one-half hour, stained in  $\frac{1}{2}$  per cent. aqueous hæmatoxylin, one-half hour, and decolorized in 4 per cent. iron alum. The fixation is very good periphally. In the brain we get some shrinkage and fragmentation of sheaths. The nerves stain well and the peripheral tissues decolorize perfectly. This is primarily an axis cylinder stain, though the sheaths can be differentiated also, if not decolorized too far.

27 *F.* The same fixation as the last. The sections mordanted in warm Erlicki's fluid for one hour; stained in warm acid hæmatoxylin one hour; decolorized in Kultschitzky's fluid. This gives a good Weigert preparation with a clear ground peripherally except near the edges.

28 *F.* Same fixation as the last. Sections mordanted one and one-half hours in warm half-saturated copper acetate, stained three hours in Weigert's hæmatoxylin and decolorized in Kultschitzky's fluid. The preparations are about like those in No. 27.

29 *F.* Fixation as before. Sections mordanted Wolter's vanadium chloride and aluminium acetate, four hours, stained in acid hæmatoxylin 3 hours, and decolorized in Weigert's decolorizer. This gives good differentiation centrally, but peripherally the muscles do not decolorize so well as in the last cases.

30 *F.* Fixation as before. Sections mordanted in Weigert's new mordant (saturated copper acetate and 10 per cent. sodium potassium tartrate equal parts) for three hours warm, followed by half-saturated copper acetate for two hours; stained in Weigert's hæmatoxylin for two hours; decolorized in Weigert's decolorizer. These are the most satisfactory sections thus far mentioned. The characteristic Weigert reaction is very brilliant both centrally and periphally and the muscles and other peripheral tissues clear well.

*Summary.*—Chrom-acetic alone cannot be applied long enough to effect any considerable decalcification without injury to the tissues, especially to the medullary sheaths. The addition of formalin (20 per cent. of the whole mixture) in large measure corrects this defect, though acids should be used rather strong, the proportions used in Flemming's stronger formula giving good results. This fixation permits excellent Weigert's preparations and promises well. I found, however, that still better results can be secured by the use of Flemming's fluid as described below; hence this line of experimentation was discontinued.

#### VI—FIXATION IN OSMIC ACID MIXTURES.

Combinations of osmic acid with nitric acid and picric acid have already been mentioned. The osmic acid mixtures which I have found most useful are (A) Hermann's fluid, and (B) Flemming's fluid.

*A.—Hermann's Fluid.*

31 *M.* Specimens fixed for from 2 to 13 days in Hermann's fluid, frequently changed, were cut and mounted directly without further staining. From 3 to 7 days seems sufficient to decalcify ordinary specimens. The tissues are thoroughly blackened, but the nerves most intensely so (except the fat), so that they can in sections easily be followed peripherally. The tissue, however, is so exceedingly brittle that I found it impossible after repeated trials to get satisfactory serial sections. Furthermore the penetrating power of the fluid is so slight that only the outer parts of the specimen are properly fixed. The brain, even when directly exposed by slicing off nearly half of the head, is always in a very bad state of preservation. Peripherally, however, the fixation of the medullate d nerves is the most perfect that I have ever been able to secure by any method, and the imperfect series which I have prepared by this method have been of the greatest use to me, especially when controlled by proper Weigert preparations for the internal courses of the nerves.

*B.—Flemming's Fluid.*

Flemming's second, or stronger formula alone has been employed. This reagent requires a rather longer time for decalcification than Hermann's fluid, from one to three weeks with frequent renewal being required for the head of a minnow. At the end of that time the tissue is, of course, exceedingly friable, but with very careful handling will hold together sufficiently to cut well and gives perfect serial sections. The fixation is all that could be desired for general purposes and the medullary sheaths are well preserved both centrally and peripherally. The smallest fibers are, however, not quite so well fixed as by Hermann's fluid. In the deeper parts of the specimen they often lose the sharpness of their contours and gelatinize more or less, probably under the influence of the other acids before the osmic acid has sufficiently permeated. The coarse-fibered components are always perfectly preserved even in the interior of the brain. The peripheral tissues are blackened somewhat but not so much as by Hermann's fluid. I had hoped to be able to mount the sections directly after this fixation without further staining, relying on the osmium precipitated in the nerve sheaths to differentiate the fibers, as has been done by others with amphibian and selachian material and as I have done with the bony fishes after fixation with Hermann's fluid. Curiously enough, however, the nerve fibers though well fixed, and that too evidently with the osmic acid, are not at all discolored, but upon dissection the nerves stand out as white cords among the blackened muscles, etc.

40 *F.* The entire head of a small adult (about 6 cm. long) was fixed for six days in Flemming's fluid. Though the decalcification was not quite complete, yet a series of sections was obtained and stained with the usual Haidenhain iron-haematoxylin (mordant in iron alum, stain in aqueous haematoxylin

and decolorize in iron alum, as in the previous cases). The fixation is very good. The medullated nerve fibers under a low power are not brilliantly differentiated, yet the high power shows them excellently preserved and the components can be followed, though not so easily as in some of the Weigert methods given below.

41 *F.* Some sections from the last specimen were stained by the method which Kenyon found so satisfactory for the insect brain (*Journal Comp. Neurology*, Vol. VI, No. 3, p. 138, 1896.) The sections were mordanted in a warm 5 per cent. solution of copper sulphate for 1 hour and stained in Mallory's hæmatoxylin,

10 per cent. phosphomolybdic acid,	1 cc.
Hæmatoxylin crystals,	1 g.
Chloral hydrate,	6 to 10 g.
Water,	100 cc.

This stain was diluted with water in the proportion of 1 of stain to 5 of water and applied for 1½ hours. The sections are considerably overstained and have to be decolorized for several hours in 70 per cent. alcohol. This gives beautiful sections of the central nervous system. The stain is rather diffuse, but cells and fiber tracts are both clearly differentiated. Peripherally, however, the muscles, etc., are so deeply stained that no differentiation of nerves is possible. This stain, though not available for my present purpose, is nevertheless a very useful one for the central nervous system. It would doubtless be improved by using the dye more dilute and applying for a much shorter time.

One section stained with iron hæmatoxylin like No. 40 was afterward stained as above. The result is not so good as either stain separately. A faint counter of the iron-hæmatoxylin sections with acid fuchsin or some similar dye, is, however, of assistance in differentiating the nerves peripherally.

43 *F.* Vassale's modification of Weigert's process. The specimen was fixed 11 days in Flemming's fluid, sections stained for 5 minutes in Weigert's hæmatoxylin and afterwards mordanted in saturated copper acetate for 3 to 5 minutes, and differentiated with Weigert's decolorizer. The nerves are not differentially stained and the sections are of little value. Other decolorizers were tried also. Pal's was still worse than Weigert's. Kultschitzky's lithium carbonate and ferricyanide of potassium gives better results, especially if the time in the stain is reduced to one half minute. The muscles, etc., are of a deep yellow color and the nerves a pale greyish blue. These are really excellent preparations and the components of the nerves can be clearly analyzed.

This rapid method invites further experimentation. I am inclined to think that with very slight modification it will give sections quite equal to the best of those obtained by the more tedious methods to be described below (e. g. Nos. 46, 53, 54.) This is a true sheath stain, but, like the other Weigert sections made after hardening in Flemming's fluid to be described next, the stain is very intense at the periphery of the fibers and very faint in the remainder of the medullary sheath, so that under a high power the effect is very different from that of the ordinary Weigert methods. The axis cylinder is a dark yellow, clearly differentiated from the sheath.

46 *F.* Flemming's fluid 11 days, sections mordanted in Erlicki's fluid 1 hour, treated with Kultschitzky's acid hæmatoxylin 2 hours and decolorized



with Kultschitzky's lithium and ferricyanide of potassium. The result is splendid differentiation both centrally and peripherally. The nerve fibers are a very intense deep blue and the ground clears well. The stain is a true sheath stain very much like that of No. 43. Cross sections show that in the case of the largest fibers the periphery of the fiber is most deeply stained and that the axis cylinder is decolorized to a clear yellow, while the intervening medullary substance is very faintly tinged with blue. Smaller fibers show the same sharp contour, but the whole of the myelin sheath is stained, though not so deeply as to wholly obscure the axis cylinder. These are, I think, the most beautiful preparations which I have secured, and, though I have not thus far used the method extensively, it will prove without doubt very useful for peripheral nerves.

50 *F.* Flemming's fluid 11 days, sections mordanted warm for  $4\frac{1}{2}$  hours in Wolter's vanadium chloride and aluminum acetate, stained in acid hæmatoxylin and decolorized by the method of Weigert. This gives very good preparations, about like No. 46, both as to the general low power effect and as to the histological appearance of the fibers under high magnification.

52 *M.* Flemming's fluid 11 days, sections mordanted in half-saturated copper acetate 3 hours, stained in Weigert's hæmatoxylin 4 hours and decolorized by the method of v. Plessen and Rabinovicz. The result is poor differentiation. The tissues clear well, but the peripheral nerves clear as soon as the muscles.

53 *M.* Specimens stained as in the last case and decolorized by Weigert's method yielded preparations which on the whole I have found most satisfactory for the purposes of the present research. The nerves are well differentiated both centrally and peripherally. The ground is not so transparent as in some of the other cases, being a light but slightly clouded brown. Nevertheless it clears well except sometimes near the outer surface where there is usually some osmic blackening. Fat is, of course, a deep black, so also are the dermal bones, while the cartilage, calcified cartilage, muscles, connective, nerve cells, etc., are of the uniform brown color. The failure of the ground to clear so as to become quite transparent is not a disadvantage, but quite the contrary, as it obviates the necessity of counter-staining, while the medullated nerves are stained so intense a blue that they can easily be followed among the other tissues, in favorable preparations even to single nerve fibers. The finest nerve fibers are not, I think, so brilliantly stained as by some of the other methods (*e. g.* Nos. 46 and 50) so that those methods have some points of superiority over this one.

The same method applied to specimens of *Fundulus* about as large as the last resulted in very poor sections. I have no doubt that further experiments upon the times and strengths of the various solutions would much improve these latter preparations; yet the *Fundulus* tissues are apparently more refractory than those of *Menidia* and I doubt if they would under any circumstances yield so good results. Small specimens of the little fresh water sun fish, *Lepomis cyanellus*, when stained by this method, give a still different color effect. The ground is a deep but brilliant bronze color which, though darker than the ground in *Menidia*, yet contrasts equally well with the blue fibers.

The general low-power effect is that of an ordinary Weigert preparation, but under a higher magnification the appearance is quite different, especially when the fibers are examined in cross section. The periphery of the fiber only

is stained, but very intensely, so that it appears quite black in the larger fibers. The deeper layers of the myelin are scarcely at all stained and the axis cylinder is decolorized to a clear yellow which is sharply differentiated from the rest of the fiber. The smaller fibers are more uniformly, but more faintly stained.

54 *M.* Specimen fixed for 11 days in Flemming's fluid, mordanted by Weigert's copper acetate and sodium potassium tartrate 2 hours, followed by half-saturated copper acetate 1 hour, stained in Weigert's hæmatoxylin and decolorized by the method of Weigert.

This method here, as after the chrom-acetic fixation, cannot apparently be used exactly as designed by Weigert, i. e. without any decolorizing, but, if properly differentiated with the decolorizer, gives preparations which are very attractive. Though I have not used the method extensively, I think it could with slight further modification be developed into a very valuable method for peripheral nerves. The sections thus far obtained are not so clear, however, as those last mentioned. The histological character of the fibers is about as in No. 46.

After the experiments above described had been performed my attention was attracted by the somewhat similar series of experiments by Bolton<sup>1</sup> in which Weigert sections of human brains were prepared after mordanting only in osmic acid, and also in a variety of metallic salts. Accordingly I instituted a few further experiments to test the applicability of such a procedure with the fish brain, with results which follow, partly under the present head and partly under the next one (formalin fixation).

55 *M.* The brain of an adult specimen was hardened four days in Flemming's fluid and after paraffin embedding the sections, without further mordanting, were stained directly in Kultschitzky's hæmatoxylin for two and one-half hours at 40° C. They refused to take up the stain at all, showing apparently that further mordanting is essential.

56 *M.* The same sections, after thorough washing in water, were treated for four hours with Weigert's hæmatoxylin at 40° C. with the same result.

57 *M.* Sections prepared as in the last case were mordanted for three hours at 40° C. in two per cent. iron alum and stained in Kultschitzky's hæmatoxylin at 40° for 20 hours. They also refused to take up the stain.

58 *M.* Sections prepared and mordanted like the last, but stained for 20 hours in Weigert's hæmatoxylin at 40° take up the stain well and when decolorized in Weigert's fluid yield fairly good preparations, though the stain is feeble. Other sections mordanted for 12 hours cold and stained for five hours give a stronger stain, and yet not wholly satisfactory.

*Summary.*—Fluids containing osmic acid give the most perfect fixation of the medullated nerves. Hermann's fluid is the best of all, and it blackens the nerve sheaths so well that sections mounted directly without further staining are the best that I have secured by any method

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<sup>1</sup> Joseph Shaw Bolton. The Nature of the Weigert-Pal Method, *Jour. Anat. and Physiol.*, XXXII, 2, Jan., 1898, p. 247.

for the separation and tracing of coarse and fine fibered components. The tissue, however, is of poor consistency for serial sectioning and furthermore cannot be stained by any of the Weigert processes which I have tried.

Flemming's fluid is the most generally satisfactory fixer. The fixation is nearly as good as that of Hermann's fluid, the decalcifying power is considerable, the tissue is in good histological condition for serial sectioning and permits a variety of excellent Weigert stains. The Haidenhain iron-hæmatoxylin (No. 40) and Mallory's hæmatoxylin after copper mordanting (No. 41) both give very beautiful sections of the central nervous system. Vassale's method (No. 43) promises well and with slight modification gives results which are nearly as good as those of the longer processes. Several of the more usual methods, after slight modification, give very excellent results centrally and peripherally, some using an acid stain (Nos. 46, 50) and some the alkaline stain (Nos. 53, 54). The most successful preparations were all mordanted in copper except No. 50 (vanadium and aluminum). The osmium in the fixing fluid is not of itself a sufficient mordant either for the acid or the alkaline dye. The stain in all of these Flemming-hardened specimens is quite unlike the usual Weigert effect, since the periphery of the myelin only is deeply stained (and this applies both in the brain and in the nerves outside), while the deeper parts of the medullary sheath are stained more feebly or not at all and the axis cylinder usually decolorizes to a yellow or brown like the general ground tissues.<sup>1</sup>

#### VII.—FIXATION WITH FORMALIN.

Most of the experiments described under this head were suggested, as intimated above, by Bolton's results with human tissue. His methods were repeated in several cases as exactly as possible, but with quite dissimilar results, as we shall see. I am indebted to my pupil, Mr. L. I. Thayer, for assistance in carrying out this series of experiments.

59 *M.* The brain was hardened in 20 per cent. formalin for six months, washed in water, embedded and sectioned in paraffin, the sections mordanted

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<sup>1</sup> It should be added that here, as usually with osmic-hardened material, the specimens should be cut soon after preservation, as a prolonged stay in alcohol is very detrimental to the staining powers. In attempting to repeat the method described in No. 53 upon specimens which had lain more than a year in alcohol I found it impossible to get even a tolerably good stain. Possibly preservation in cedar oil would remove this difficulty, though I have not as yet tried it. The safest way to preserve for long periods is unquestionably to embed and leave in the block.

for 12 hours in saturated copper acetate and treated with Weigert's hæmatoxylin for six hours. They took up the stain only very faintly.

60 *M.* Mordanting for 16 hours in 5 per cent. potassium bichromate and treating for 12 hours with Weigert's hæmatoxylin gave the same results.

61 *M.* Mordanted similar sections in saturated copper acetate for 12 hours, washed and then treated for 16 hours with 5 per cent. potassium bichromate and stained for 12 hours with Weigert's hæmatoxylin. They take up the stain to some extent, but upon applying Weigert's decolorizer the white matter bleaches before the grey. I reversed the order of the mordants, first the bichromate, then the copper, with the same result.

Osmic acid, iron alum and ammonium molybdate are the three mordants which Bolton found to give the most satisfactory results with the human brain after six months hardening in 5 per cent. formalin. To test their value with the fishes the following experiments were tried:

62 *M.* The brain, which had been hardened for five months in 10 per cent. formalin, was washed in water and sectioned in paraffin. The sections were mordanted for 15 minutes in 1 per cent. osmic acid, stained for 15 hours in Kultschitzky's acid hæmatoxylin and decolorized by the method of Weigert. This gives a diffuse brown stain with the nerve fibers not at all differentiated.

63 *M.* Other sections were given the same treatment save that they were stained in Weigert's hæmatoxylin. The result is similar, the stain not being quite so intense.

64 *M.* Sections prepared like the last were mordanted for 14 hours in 2 per cent. iron alum, stained in Weigert's hæmatoxylin and decolorized by the method of Weigert. This gives a stain similar to the last, though both cells and fibers are slightly better differentiated.

65 *M.* As before, but stained in Kultschitzky's hæmatoxylin, and with the same unsatisfactory result.

66 *M.* Similar sections were mordanted for 14 hours in 2 per cent. ammonium molybdate and stained in Kultschitzky's hæmatoxylin. They took the stain only faintly and the fibers decolorized wholly, leaving all nuclei vividly stained.

67 *M.* Like the last, but stained in Weigert's hæmatoxylin. They decolorize wholly with no differentiation.

The six cases last given resemble Bolton's best methods, save that he differentiated by the method of Pal. Having found that in several of these cases that method gave still worse results than the method used, I conclude that none of these methods are adapted to fish tissues. Being very desirous of utilizing formalin hardening material, I next tried several modifications of the method used by Edinger in his studies upon the reptile brain.

68 *M.* The brain, which had been hardened for five months in 10 per cent. formalin, was washed in water and then soaked for six days in Weigert's fluid,

Water,	100 cc.
Potassium bichromate,	5 g.
Chrome alum,	2 g.



The sections, cut after paraffin embedding, were mordanted for five hours in warm copper acetate two-thirds saturated, and stained in Kultschitzky's hæmatoxylin for 12 hours. They did not take up the stain properly.

69 *M.* Another specimen was prepared exactly like the last save that the alkaline hæmatoxylin (Weigert's) instead of the acid stain of Kultschitzky's was used. The sections take up the stain well and when decolorized by the method of Weigert give excellent differentiation.

These sections have a very different appearance from any of the Flemming hardened specimens. The fibers under the high power exhibit the more usual appearance of ordinary Weigert sections, *i. e.*, the fibers, both large and small, are stained a deep blue black, the entire myelinic sheath and the axis cylinder being uniformly colored. Upon further decolorizing the axis cylinder is left deeply stained after the myelin has been almost completely cleared. This is, then, an axis cylinder stain, as well as a myelin stain; the naked collaterals and terminal arborizations seem to take up and retain the dye and the "Punksubstanz" is always tinged with blue. All nuclei also retain the color. This, then, is a very useful stain for fishes, as well as for reptiles.

*Summary.*—Brains hardened in strong formalin have the nerves well fixed, though not so faithfully as osmium hardened specimens. It is an interesting fact that those methods which in Bolton's hands gave the best results upon the human brain fail utterly when applied to fish brains. This is doubtless due to chemical difference in the tissues, for it is well known to all who have worked with the more delicate staining methods that even closely related animals often require different treatment. It is, however, possible to get excellent Weigert preparations of fish brains that have been fixed in formalin by using the method of Edinger (No. 69).

#### VIII.—FIXATION IN VARIOUS SALTS.

As previously mentioned, the bichromate of potash, which is commonly used as a fixer for Weigert sections, does not preserve the nerve sheaths with sufficient fidelity for my purposes. Strong formalin is, however, a good preservative of nerve sheaths and it was tried in combination with several salts which are known to act favorably as mordants.

72 *M.* A young specimen was fixed for 5 days in a mixture composed of iron alum 4 per cent. and formalin 10 per cent. Without further mordanting the sections were stained in one-half per cent. aqueous hæmatoxylin for three-quarters of an hour and decolorized by the method of Weigert. The result was no differentiation whatever.

73 *M.* Other similar sections stained in Weigert's hæmatoxylin for 15 hours and decolorized in 2 per cent. iron alum gave even worse results.

74 *M.* Still other sections stained in acid hæmatoxylin and decolorized in 4 per cent. iron alum differentiated the nerve fibers quite well, though not so well as the following.

75 *M.* The best results were obtained by fixing as above, staining in one half per cent. aqueous hæmatoxylin for one hour or more and decolorizing in 2 per cent. iron alum. This gives very brilliant Weigert preparations.

This fixing fluid was devised and suggested to me by Dr. Oliver S. Strong, who has applied it very successfully to the amphibian brain. The fixation is not so perfect as that of the osmic acid mixtures, but better than the usual bichromate. Moreover, it has a very considerable decalcifying power, a point of no small practical value. My specimens of young, but nearly full grown, minnows were fully decalcified after 5 days' treatment. The stain is absolutely differential, the ground both centrally and peripherally becoming almost perfectly transparent. All nuclei, however, resist the decolorizer more or less, though usually not so much as the nerves. The latter are of a very brilliant light blue color, the dye being confined to the periphery and the axis cylinder of the larger fibers, but staining all of the myelin of the smaller ones. The sections are of exquisite beauty; unfortunately, however, the fixer leaves the tissue very brittle and of a very poor consistency for cutting. This is an insuperable objection to its use in the study of the peripheral nerves, as I have never been able to get satisfactory continuous sections through the whole head. In the case of brain or spinal cord this disadvantage is not so serious.<sup>1</sup>

76 *F.* A small specimen was hardened for 8 days in the following mixture:

Chrome alum, 4 per cent.,	45 parts.
Iron alum, 4 per cent.,	45 parts.
Formalin,	10 parts.

It was then left in 10 per cent. formalin for a week and embedded and sectioned. The sections were stained in aqueous hæmatoxylin and decolorized in iron alum, as in the preceding case. The fixation is about as before and the stain very similar, though the ground does not clear well. Other decolorizers were not tried. The tissue seems to be in much better histological condition than that fixed in formalin and iron alum alone, and the method merits further study.

*Summary.*—None of the mixtures of formalin and the metallic salts give wholly satisfactory results. Either the fixation is not perfect or the tissue is of poor consistency for cutting. The most valuable combinations which I have tried are mixtures of formalin and iron alum and formalin, iron alum and chrome alum. These fluids fix well, have considerable decalcifying power and yield the most brilliant sheath stain (and the former the most transparent ground) which I have obtained by any method.

This pre-eminence of the iron alum as a mordant accords with

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<sup>1</sup> Since the publication of this article Dr. Strong writes me that sections of old embryos of the smooth dog-fish, *Galeus canis*, fixed in the iron-alum-formalin and stained without further mordanting in aqueous hæmatoxylin, decolorized with 1 per cent. iron alum are very fine. The fixation is admirable, especially the connective tissue, which is perfect (probably due to the formalin).

Bolton's results with human tissue, though it is noteworthy that his finest preparations were obtained by simply mordanting for a short time sections of the formalin-hardened brain, while with the fish tissues this method in my hands gave negative results and the tissue must be fixed, as well as mordanted, in the iron salt.

#### CONCLUDING REMARKS.

Extended commentary upon these experiments is unnecessary, as the results speak for themselves so far as practical utility is concerned and it is not my purpose to enter into an elaborate discussion of the theory of the Weigert stain. The ground covered in the experiments was, as has been stated, determined wholly by the practical requirements of a definite research; nevertheless the peculiarities of the tissues upon which the work was done are such as to cast some light upon the nature of the staining processes.

In this research I have found, as others before me have done, that the fish tissues are refractory to a surprising degree. This does not accord with my own earlier experience, for, in the course of the preparation of an extended series of teleostean brains by ordinary methods (especially Delafield's hæmatoxylin) made several years ago in connection with my brother, it was easy to obtain the most elegant preparations,—preparations which could not be excelled in any other group of vertebrates. But in the present case there were not only the special difficulties mentioned in the introductory paragraphs, but the presence of the body musculature in the sections imposes other peculiar conditions. It seems that the teleostean muscles and the myelinic nerve sheaths react toward the hæmatoxylin stains very similarly, for they decolorize at very nearly the same time. It was found, for example, in every case where the decolorizer of Pal was tried that the nerves clear before the muscles and in other cases they often clear at about the same moment. This peculiarity destroys the value for peripheral nerves of a number of processes which are very satisfactory centrally. It also sheds some light upon the nature of the staining process.

In the paper by Bolton to which reference has already been made, this author concludes, as a result of an extensive series of experiments upon human brain tissue which had been hardened for several months in five per cent. formalin, that, "the Weigert-Pal process is not a specific method for the staining of medullated nerve fibers with hæmatoxylin but is a method of dyeing fibrils which comprises three distinct operations: the mordanting of the fibers, the formation of a lake in them, and finally, the removal of the stain by oxidation from nearly every other part of the complex tissue under treatment."

This in general I confirm, and also agree with him in finding that other besides nerve tissues may take up and retain the dye, such as blood corpuscles, and the nuclei and especially the nucleoli of nerve cells. The illustrations which he gives of fibers mordanted in chrome alum and in osmic acid (his Fig. 2) show that only the outer zone of the myelinic sheath is stained, the general effect being similar to the Weigert's specimens which I prepared after fixation in Flemming's fluid and mordanted in copper (e. g. No. 53), though it should be noted that all his figures show that the fibers were very badly fixed in his preparations. The differences in the intensities of stain and colors of the nerve sheaths in Bolton's preparations he attributes to the differences in the mordants and in this he is doubtless in the main correct, for he employs only one kind of stain (the acid hæmatoxylin) and only one mode of decolorizing.

Now, the failure of any tissue to stain by the Weigert process may be due either (1) to the fact that it does not take up the mordant and hence does not form the lake, or (2) to the fact that the lake formed is there more readily oxidized than the other tissues which resist the decolorizer. The first point is emphasized by Bolton—unduly so, as it seems to me. He says, "Just as fine glass threads included in a web would not stain, so nearly the whole of the fibers in the body excepting those belonging to the neurons, do not stain owing to the fact that they refuse the mordant and consequently the lake." But in my experience—and this applies especially to sections containing general as well as nervous tissues—as a rule either the whole section refuses to stain or all of the tissues take it up intensely, and with the slower methods of decolorizing it is clear that the stain is not merely upon, but is in the tissue elements. It must be admitted that all of these non-nervous tissues, except the blood corpuscles, stain black, not blue, and it may well be that they do not form the same kind of a lake as the myelin of the nerve sheaths. But this applies also to the axis cylinders and to the muscles, in both of which, I infer, Bolton considers that a true lake is formed. The fact that some mordants refuse the acid stain but under the same conditions take up the alkaline stain and conversely, leads me to believe that a failure to stain may quite as often result from a chemical peculiarity of the tissue after it is mordanted as from a refusal of the mordant.

And this leads to the second point. If the lake is formed, what is it which determines whether it will be more rapidly oxidized in one tissue than in another? Bolton believes, apparently, that this condition is simply the permeability of the tissue, "the parenchymatous part of



the sections being naturally more readily permeable to the oxidizing agent than the bundles of fibrils, and consequently more readily decolorized." That this principle operates to a certain extent must be admitted, yet it must play a very subordinate rôle. It would, I think, be difficult to convince anyone who has watched the differentiation by one of the slower methods of Weigert sections cut through the entire body and containing various kinds of tissue that the rate of decolorizing is proportional, however roughly, to the permeability of the tissue. It ill accords with such a view to find that the deeper layers of the myelin sheaths clear before their periphery, that the axis cylinder sometimes decolorizes to a clear yellow still earlier in the process, that the nucleated blood corpuscles of the fishes (a tissue which is certainly sufficiently permeable) may retain their brilliant blue color after all the nerves are fully decolorized and the large muscle fibers, transversely cut and hence with their protoplasm directly exposed to the action of the reagents, decolorize nearly as late as the medullated nerves and sometimes even later. On the contrary these variations rest upon chemical differences in the tissues which cause them to react differently to the dye. That it is not merely a question of permeability, is clearly shown by the fact that a change from one decolorizer to another is often sufficient to cause a reversal of those conditions, *e. g.*, to cause muscles to decolorize before instead of after the nerves. Such chemical differences, not only between different tissues, but between the same tissue in different animals, are real factors, as is shown by the fact that histological methods which yield a satisfactory stain, say in the Amphibia, may fail completely when applied to the fish, and that even different species of fishes have not the same susceptibility to stains. This receives the most frequent illustration perhaps among workers with metylene blue. These staining reactions are far too complicated to be reduced to chemical terms until we know much more of the chemistry of the tissues which take up the stains than we do at present.

I desire in conclusion to express my deep obligation to Dr. Oliver S. Strong for advice and valuable suggestions freely given in the course of these researches.

C. J. H.

## PATHOLOGY.

### Mills' Practical Neurology.<sup>1</sup>

American science is to be congratulated in having been the first to supply a comprehensive treatise on neural pathology in terms of the

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<sup>1</sup>CHARLES K. MILLS. *The Nervous System and its Diseases*. J. B. Lippincott and Co., 1898.

modern neurology. This work is not only comprehensive and exact but it is conceived in the light of the recent discoveries which have transformed our conceptions of structure and function of the nervous system. It is not to be expected that a work devoted to pathology should furnish an exhaustive account of the details of anatomy and histology but it may be frankly admitted that the introductory chapters in the book before us constitute a better general guide to the student of these subjects than any English treatise we are familiar with. Where the mass to be selected from is so large and the difficulty of harmonizing discordant results is so great we could have condoned many imperfections and have only praise for the discriminating way in which the extraordinarily wide field has been gleaned. Occasionally the English is not quite smooth, as where the cranial nerves are said "to come and go from the encephalospinal centres" and where the entering fibers divide within the central system "into T-shapes," and it seems to us that the dignity of the work suffers, without really enhancing its usefulness, by a somewhat condescending tone toward the reader who, nevertheless, is assumed to be competent to follow the author through the intricacies of one of the most difficult branches of descriptive science.

The nomenclature is that of Dr. Wilder throughout and as such will give offence to those whose prejudices are now filling the journals with personal abuse of the founder of that system. But in view of the fact that this is the only complete system of nomenclature at present before the public and the only one which is self-consistent and carefully elaborated in its details, the author who, is writing a comprehensive work for practical use in the hands of busy men, is ambitious to have his description formulated in brief and unambiguous language very naturally preferred to accept what already exists to the necessarily unsatisfactory attempt to formulate for himself out of scattered shreds and patches an eclectic system. It seems to us that most practical men who find their prejudices irritated by some of these terms will concede that the author has pursued a reasonable course and that by supplying a running glossary of other terms used by various authors the greatest good of the greatest number has in this case been subserved. The introductory chapter devoted to the anatomy and physiology as such comprehends 125 pages and is amply illustrated but the illustrations introduced in connection with the pathological descriptions greatly add to the scope of even this generous allotment. The discussion of the normal physiology is we think the weak part of the book and hope it may be possible to extend this section in future editions.

The book is strong on the practical side. The accounts of the methods of aësthometry and tests of motor insufficiency are full and the introduction to electro-therapeutics is apparently very complete, as is the part devoted to massage and vibratory therapeutics. Rules for postmortems will prove helpful to many a busy man. Cortical localization and operative indices are accorded commensurate attention without slighting the descriptive pathology.

Dr. Mills quotes with apparent approval the extreme ground taken by Dr. Bevan Lewis as to the rôle of the scavenger cells in cerebral disease, where more attention should probably be given to the vascular changes and the wandering cells. He also adopts the view of Retzius and others that the olfactory and optic nerve endings form a class distinct from that including the gustatory, tactile, and auditory on the other hand. There is much reason to believe that this classification is based on a misconception.

But while it would be easy to suggest other instances where there is room for difference of opinion as to the details of the work, we have for the book as a whole only warm praise and congratulate both the author and the publisher on the results of their efforts. We shall have further commentary to offer upon this important work from a different point of view in a later issue of this Journal.

C. L. H.

#### **Chapin's Compendium of Insanity.<sup>1</sup>**

This little book is designed to present a concise statement of the clinical aspects of the various abnormal mental conditions, together with plain directions as to the best methods of managing and treating the insane. It is conservatively written, really too much so in some places even for an elementary manual designed to introduce the medical student to psychiatry, as illustrated for instance, by the antiquated treatment of the pathology of the so-called functional diseases. It is an excellent work, however, the chief value of which will be to give the lay reader who desires to inform himself upon these subjects a concise and intelligible guide, and for this purpose the book can be cordially recommended.

C. J. H.

#### **Genesis and Nature of Hysteria.<sup>2</sup>**

This important work, comprising some 850 pages, is divided into two parts, one of which (volume I) is a systematic presentation of the

<sup>1</sup> A Compendium of Insanity. By John B. Chapin, M.D. Philadelphia: W. B. Saunders, 1898. \$1.25 net.

<sup>2</sup> Genèse et Nature de l'Hystérie. Dr. Paul Sollier. 2 volumes. Paris, Félix Alcan' 1897. Price 20 fr.

author's conclusions regarding the course, nature and etiology of hysterical affections, while the second volume is devoted exclusively to the detailed record of twenty cases from the author's practice, narrated as fully as possible and uncolored by interpretation or theory. The data of this second part are analyzed in the first part under the following headings: I. Généralités; II. Réactions liées au réveil de la sensibilité; III. Interprétation des accidents somatiques; IV. Interprétation des accidents mentaux; V. Interpretation des stigmates hystériques. Then follows the synthetical grouping of all of the facts in the development of a *General conception of hysteria*..

C. J. H.

### Neuro-Pathology and Heredity.<sup>1</sup>

The first edition of Dr. Féré's work we have before noticed. [This Journal Vol. IV, p. clv]. This second edition is somewhat enlarged, the most important additions being found in the chapters devoted to teratological heredity, the relations between malformations and morbid predisposition and experimental teratology. A chapter is added on the morbid heredity of tumors. The book is well indexed, and abundantly furnished with bibliographical references.

Degenerescence, from whatever cause, the author defines as a dissolution of the conservative forces of heredity which terminates ultimately in sterility. The treatment of the stigmata of degenerescence is good. Their value is recognized and properly estimated, i. e., the stigmata, so far as they are truly such, are indicative of a general weakening of the organization and in the nature of the case cannot be expected to run true to type. It is not therefore possible to define types of mental or moral degeneracy in terms of any particular set of physical stigmata, for such stigmata are common to all types of degeneracy.

C. J. H.

### Fleury's Mental Medicine.<sup>2</sup>

This work is not, as the title might lead one to suppose, an introduction to mental pathology; but rather a series of essays on medicine

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<sup>1</sup> La famille névropathique, théorie tératologique de l'hérédité et de la prédisposition morbides et de la dégénérescence, by Dr. Ch. Féré, médecin de Bicêtre, 1 Vol. de la *Collection Médicale*, 4 fr. Deuxième édition revue et augmentée. Paris; F. Alcan, éditeur, 1898.

<sup>2</sup> Introduction à la Médecine de l'Esprit. DR. MARUICE DE FLEURY, ancien interne des hôpitaux. 1 vol. in-8°, 7 fr, 50.—Paris, Félix Alcan éditeur. 1897.



and morals which might better be entitled "Introduction to Modern Morals." We can indicate its scope no better than by quoting the titles of the chapters. First Part—*L'enseignement de la Salpêtrière ; les médecins et la justice ; les médecins et la littérature ; les médecins et la psychologie ; la fatigue et la force humaines.* Second Part—*la paresse et son traitement ; la tristesse et son traitement ; la médecine de passions ; la colère et son traitement ; la morale moderne.* C. J. H.

### **The Truth About Cigarettes.**

Under the above title a brochure has come to our table with a request for a notice which is, as its subtitle justly intimates, a "brief for the cigarette". The paper offers interesting figures for the consideration of the humanitarian and layman as well as the physician. The annual output of cigarettes for the year will, it is estimated, reach 4,000,000,000, and if the cigarette is really the beneficent thing we are allowed to infer it must be, we should rally to the support of this infant industry and "put a stop to the idle detraction and senseless legislation directed against an evil wholly imaginary."

We are assured that responsible dealers not only do not add arsenic, opium, morphine, phosphorus, copper or any other poisons to the principle ingredient but that the paper used is "at most somewhat irritating to the respiratory mucous membrane." A number of transparent falsehoods are impaled, but to one familiar with the effects of the cigarette on the young, the paper suggests the old legal maxim: "suppressio veri, suggestio falsi." C. L. H.

### **MISCELLANEOUS.**

#### **The Journal of Applied Microscopy.**

The above mentioned periodical promises to make a useful place for itself. It is devoted chiefly to technique and its list of contributors is of a character to guarantee excellence in this line: As a rule we prefer to find the description of the method in connection with the results obtained through its use and hope that this side of the field may not be neglected. In the April number two papers of special use to the neurologist are to be noted: *The Rosanilin Dyes—Their Relation to Microscopy*, by V. A. Latham and *The Methylen Blue Method for Staining Nerve Tissues*, by G. Carl Huber. The subscription price is so reasonable that there should be a large list of subscribers.

C. L. H.

**Neurologic Terminology.<sup>1</sup>**

If we may judge from a number of recent publications on nomenclature, in the minds of some at least, a critical point has been reached in neurologic terminology in America in the recent report above indicated. This is the last and most radical step in the direction of a simplification of existing anatomical nomenclature that has so far been made.

The committee appointed by the Association of American Anatomists had previously made preliminary reports in 1889 and 1895 which are embodied also in the present report. In addition to the Association of American Anatomists, reports on Anatomical Nomenclature have been adopted by the American Association for the Advancement of Science in 1889, '90 and '92, and a more comprehensive report by the committee of the American Neurological Association in 1896. All of these embody the same tendencies and principles in nomenclature which in the report now before us are given a broader application and carried to a greater extent. In preparing the present report of the Association of American Anatomists there has been a sharp divergence of opinion in the committee; hence the list of recommendations offered is presented by the majority of the committee composed of Prof. F. H. Gerrish of the Medical School of Maine; Prof. G. S. Huntington of the College of Physicians and Surgeons of New York, and Prof. B. G. Wilder of Cornell University; against which report are voiced the protestations of the minority,—Prof. Dwight of Harvard Medical School, and Dr. Baker of Washington. It should be further noted that the list of the majority is based upon the list of terms recommended and employed by the secretary of the committee, Dr. Wilder, as published recently in this Journal (Neural Terms, National and International). The only other list published by an association of anatomists is the report of the German Nomenclature Commission adopted by the *Anatomische Gesellschaft* in 1895 embodying a list of some 500 neural terms which are recommended for use.

As compared with the list of the German Nomenclature Commission, which aims to present a complete system of nomenclature for human anatomy, the report adopted by the Association of American Anatomists is a fragment; it comprises 475 terms which may be grouped as follows: 23 terms identical with those of the German Commission; 78 which are the same as those of the German

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<sup>1</sup> Reports of the Majority and Minority of the Committee on Anatomical Nomenclature, and Comments of the Secretary of the Committee. *Proc. Assoc. Am. Anatomists*, 10th Annual Session, December, 1897, pp. 27-60.

Commission but with some difference of meaning; 15 terms previously adopted by other American Societies; and 259 that have not been adopted by any society hitherto. Compared also with the German list, the recommendations of the American Association are possibly less representative of existing usage by anatomists, especially human anatomists.

The aim throughout has been the adoption of terms which accord with the principles of nomenclature laid down by the Committee on Biological Nomenclature of the American Association for the Advancement of Science, and when contrasted with older usages, there are many differences which in general are also simplifications. In most cases, this is due to either (a) a reduction of terms of two (or more) words to a single word term by dropping one of them as unessential,—generally the substantive; or (b) by incorporating the adjective with the noun as a prefix. In some few instances the German Commission had introduced the same simplification by dropping a useless word, as *thalamus* (*opticus*) *pons* (*Varolii*) etc. The employment of dorsal and ventral for posterior and anterior should also be emphasized. In a large number of cases, the terms are essentially distinct from those generally accepted, and are employed apparently by but few neurologists. In general, however, they have the recommendation of brevity and are descriptive or locative.

A judgment of the recommendation as a whole is rather difficult; where there is departure from the recommendations of the German Nomenclature Commission, it is generally in the direction of a simplification purchased often by the introduction of new terms not recognized by general usage. "General usage," it must be remembered, however, has in many cases no real existence. Indeed, the fact that committees of societies have been appointed in Germany, England and America for the regulation of anatomical nomenclature evidences the need felt by working anatomists, of a uniform system of appropriate terms. Many of the terms generally employed are admitted long and unwieldy, and the attitude of American Anatomists toward the present recommendations must be determined by the recognition that it is the difficult question of in how far it is best to supplant that which is older by that which may be better,—abstractly considered; and if changes are needed, how rapidly may they be wisely introduced. It is the old antagonism of radicalism and conservatism.

The report of the Minority offers nothing that can afford help. It contains no comment upon any term or group of terms, but consists simply in a general protest against what is termed "Dr. Wilder's Sys-

tem." The introduction of the personal element is much to be regretted. The existence, or at least the personality of the other members of the Majority, Drs. Gerrish and Huntington, is apparently ignored, and there is no recognition of a tendency toward a simplification in terminology such as certainly exists nowhere in this country aside from the personality of one man, to whomsoever it may have been due primarily, as is illustrated by the terminology employed in some recent books such as Mills' Diseases of the Nervous System and Parker and Haswell's Zoology.

The entire matter will be reopened at the next annual meeting, it is promised; and it is to be hoped that personalities may be hereafter entirely eliminated.

B. F. K.

**Errors and Omissions Detected in the Reproduction of the "Neurologia" portion of the "B. N. A." (Basel Nomina anatomica)\* in B. G. Wilder's "Neural Terms."†**

*Interpolations.*—A certain number of parts or features had not apparently been designated in the B. N. A. What were supposed to be the names that would have been employed were introduced by me. These interpolated terms were intended to be in brackets, but this feature was sometimes omitted accidentally. Since, also, three terms were already bracketed in the B. N. A. (p. 313, 35, 36, 37) misapprehension might arise. The following terms do not occur in the B. N. A. and should be marked out of my List.

P. 302.—8.—Liquor cerebrospinalis.

P. 293.—16.—Ventriculus olfactorius. 17.—Pars olfactoria foraminis inter-ventricularis. 18.—Pars anterior commissurae anterioris. 8.—Gyri operati. 9.—Gyri operientes. 11.—Fissurae cerebri. 12.—S. et F. operati. 13.—S. et F. operientes. 15.—Impressio confluentis. 21.—Pars basilaris. 24.—Pars anterior. 25.—Pars posterior. 26.—Sulcus centralis insulae.

P. 304.—31.—Hilus insulae. 36.—Pars orbitalis. 46.—Sulcus centralis inferior. 41.—G. transitivus centralis. 42.—G. transitivus profundus centralis. 44.—Pars postfrontalis. 45.—Pars praefrontalis. 47.—Pars superior. 48.—Pars inferior. 54.—Sulcus frontalis intermedius

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\*Die anatomische Nomenclatur. Nomina anatomica, Verzeichniss der von der Anatomischen Gesellschaft auf ihrer IX. Versammlung in Basel angenommenen Namen. Eingeleitet und im Einverständniss mit dem Redactionsausschuss erläutert von Wilhelm His. *Archiv für Anatomie und Physiologie*, Anat. Abth., Supplement Band, 1895. O, pp. 180; 27 Figs., 2 plates.

†Neural Terms. International and National. *Journal of Comparative Neurology*, VI, December, 1896, pp. 216-225, including seven tables. Parts VII-IX have also been reprinted under the title "Table of Neural Terms, with Comments and Bibliography."



P. 305.—86 to 93 inclusive. 94.—(Duplicate of 84). 97.—Sulcus intermedius. 98.—Sulcus exoccipitalis. 99.—F. calcarina externa.

P. 306.—115.—F. occipito-calcarina. (The inadvertent omission of the brackets is much regretted). 116.—Postcalcarina. 118 to 123 inclusive. 1 to 3 inclusive.

P. 307.—37.—Indusium. 45.—Crista. 46.—Carina.

P. 311.—34. | Tractus pedunculi transversus. 1 and 2.

P. 312.—23.—Sulcus praeclivalis. 31.—Lobulus gracilis. 38.—Folium cacuminis. 41.—Fossa praepeduncularis. (If anything this should have been Fossa brachii conjunctivi),

P. 312.—31 and 33.

P. 314.—1.—Cavitas communis myelencephali et metencephali. 16.—Hordea. 26.—Pars myelencephalica ventriculi quarti.

P. 318.—21.—Leptomeninges. Also 33 to 35 inclusive. 8.—Cerebri anterior media.

P. 319.—A, 12, 14 and 15. B, 4 and 5.

*Omissions.*—P. 302.—Under *Rhinencephalon*, 3; after *Gyrus subcollosus* should be, in brackets, *Pedunculus corporis callosi*.

P. 305.—Between 13 and 14 should be *Sulcus temporalis inferior*. Between 108 and 109 should be *Gyrus hippocampi*.

P. 311.—Between 13 and 14 should be *Lemniscus*. Between 15 and 16, *Trigonum lemnisci*. After 36 should come *Ganglion interpedunculare* and *Nucleus n. trochlearis*. The name *Isthmus rhombencephali* should occur on this page.

P. 312.—Between 30 and 31 should be *Tonsilla cerebelli*.

P. 313.—After 42 should come *Hilus nuclei dentati* and *Capsula nuclei dentati*.

P. 314.—After 4 should come *Recessus lateralis fossae rhomboideae*.

P. 315.—After 13 should come *Hilus nuclei olivaris*.

P. 316.—After 12 should come *Sulcus intermedius posterior*.

P. 317.—After 12 should come *Arachnoidea spinalis*.

*Other errors.*—P. 302.—16.—For *Nervus* read *Ramus*. Under *Rhinencephalon*, in 6 and 7, the parentheses should be brackets. 11.—For *lateralis* read *anterior*.

P. 306.—II, B.—For *Corum* read *Eorum*.

P. 307.—49.—Omit the brackets.

P. 308.—30.—For *striata* read *striati*. III.—After *Diencephalon* omit *et Thalamencephalon*.

P. 310.—26.—*Mamillaris* should be *mamillares*.

P. 312.—13.—*Lobus* should be *lobulus*. 45.—*Pontis* should be in brackets. 46.—The entire term should be in parentheses.

P. 313.—22 and 23.—*Sensitivus* and *acusticus* should be in brackets. 42.—*Globuliformis* should be *globosus*.

P. 314.—6.—F. r. (for Fossae rhomboideae) should be in brackets.

P. 315.—25.—In the original there is no dieresis.

P. 316.—13.—*Sulcus intermedius anterior* should be in parenthesis.

P. 317.—6.—*Sellae* should be in brackets. 13.—*Arachnoideale* should be *arachnoideale*. 14.—The last syllable should *es*.

In the body of the paper, besides the corrections enumerated on p. 352, on p. 224, § 40, *Magniloquy* should be *Magniloquy*.

BURT G. WILDER.

Ithaca, N. Y., March 30, 1898.

## CRITICAL DIGEST.

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### REVIEW OF RECENT TEXT-BOOKS OF ANATOMY AND PATHOLOGY OF THE NERVOUS SYSTEM.

#### FIRST ARTICLE.

Neuropathology enjoys a great advantage over other branches of pathology; the text-books of anatomy, histology, physiology and pathological anatomy are notoriously so deficient as a basis for clinical neurology and the special treatises with few exceptions so little adapted for diagnostic studies that almost every writer is allowed to give his own normal neurology in the way of an introduction to his anatomical and clinical pathology. Other branches of medicine have been prematurely weaned. How little is said of the normal heart and mechanism of circulation, of the normal respiratory apparatus etc., in the corresponding treatises of pathology—and how little does the ordinary text-book of physiology know of the doubts and difficulties of the practitioner! It would be stupid to ask physiologists and anatomists to limit themselves in their text-books to what the clinicians need or even to lay special stress on the methods of the clinicians; the latter must attend to that themselves. Anatomy, physiology and psychology must exist and be cultivated as independent sciences; but the clinician should be able to select from them the essential material from his utilitarian, practical standpoint.

One of the strongest negative illustrations of this point within the field of neurology is a volume on the normal spinal cord by *Ramon y Cajal* in the wonderful series of Babes etc., *Atlas der pathologischen Anatomie des Nervensystems*. The famous Spanish histologist seems not to have the slightest inkling of what the student of pathological anatomy needs most to know concerning the normal spinal cord. How much more satisfactory would it have been if an experienced pathologist had given normal pictures of points difficult in the practical work—comparisons of various parts and tissue-elements of the cord, of individual variations, the conditions of different ages etc.—made with methods applicable in pathological research. Instead of this we get cord-sections of the embryo chicken and mouse and one desper-

ately diagrammatic human section. Who will ever profit from such a description of the normal where comparisons with possibly pathological conditions in other parts of the atlas or in his own specimens are desired?

v. Monakow<sup>1</sup> has made excellent use of his opportunity. His '*Gehirnpathologie*' contains a concise and well considered summary of anatomy of the brain, its physiology, general pathology and the clinical symptoms of organic brain disease (p. 1-375). He then passes over to problems of diagnostic localization (p. 376-666) and discusses the principal disorders of the circulation; hemorrhage (p. 667-792), occlusion of arteries (p. 793-876), and sinus-thrombosis (p. 877-894). This is the first part of Vol. IX of Nothnagel's Special Pathology and Therapy. It is one of the few books which deserve complete reading by the reviewer because one has the feeling that a man of experience speaks of things with which he is familiar and if criticism of detail is provoked in a few portions of the work one may give it without fear of hurting publisher or writer. There are so many good points that an enumeration of possible defects does not detract from the deserved admiration.

v. Monakow starts with a short sketch of the early embryology, and insists on the importance of an independent growth of two parts of the nervous system; the sensory proton (the sense-organs and the vegetative nervous system) on the one hand and on the other, the motor apparatus with the rest of the 'central' nervous system; illustrations of this are seen in anencephaly, amyelia etc. In the sketch of the development of the brain-vesicles, the formation of 'five vesicles' out of the three fundamental enlargements of the neural tube deserves criticism as incorrect, though sanctioned by long tradition; the forebrain consists of the one original enlargement of the neural tube (primary forebrain) with two hemisphere-protrusions; why should these two protrusions be called one vesicle on ground of the arbitrary existence of a 'cella media'? A similar objection holds for the division of the rhombencephalon. How can we speak of two 'vesicles' if at the level of the dividing line (in the *adult* the lower end of the 'pons') the lumen of the tube is widest? The division into three enlargements and accessory pockets is much more correct and didactically clearer. The laws of development are very hastily mentioned and the sequence of development suggested on physiological grounds—vegetative life,

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<sup>1</sup> *Gehirnpathologie* von Dr. C. v. Monakow, Zurich. mit 211 Abbildungen. Wien, 1897, Alfred Hölder.

sensation, reflex-motion (kicking, sucking, swallowing), finally higher senses and movements under mental control—would hardly stand criticism and should be replaced by the facts of anatomical development, as a help for the study of neuropathology in the foetus and child. Following Schaper and others, v. Monakow correctly avoids the traditional 'spongioblasts' and 'neuroblasts' and reserves the latter name for the developing 'neurone.'

On p. 8, v. Monakow mentions an extensive communication between the hemisphere-cavities and the brain surface; the two hemisphere-vesicles are first open and later closed by the corpus callosum towards the end of the 4th month; the mesial and posterior 'gaps of the hemisphere-wall' are 'closed' in a similar way by the growth of the fornix. This description, though preceded by a correct statement of the nature of the choroid plexus, is quite misleading, and as it stands, incorrect. Finally we should object to the statement on p. 9, that the first foldings of the hemisphere occur around the island; the folding of the hippocampal fissure and the parieto-occipital-calcarine complex appear long before the 'three principal branches of the Fissura Sylvii,' which are not folds in the same sense but produced by overlapping of the mantle over the stem. In a second edition or a translation, this embryological part might well be lengthened a little, as it might easily form the back-bone for the general morphology and furnish important data for the pathology of the developing nervous system only partly treated by v. Monakow.

Pp. 11-25 are devoted to the fissures and convolutions of the fore-brain. v. Monakow strongly insists on the amount of cortex which lies *in* the fissures. We miss a statement of the interlocking of the central fissure and the supra-marginal sulcus, an exceedingly useful point for general orientation. Only once in over 300 of my autopsies the central fissure did *not* reach the upper edge of the hemisphere, as is pictured in fig. 5 and 6. In the brain mentioned (coming from an average woman with alcoholic insanity) the 'paracentral lobule' contained no Betz cells; they were found more laterally; this (and other facts) would lead me to expect a more intimate relation between internal cortical structure and configuration of the fissure than v. Monakow admits on p. 12.

In view of the fact that the description of convolutions and even of fissures varies from brain to brain, it might be advisable to give up a detailed description to text-books of anatomy and anthropology and to insist more emphatically on typical land-marks customarily used in autopsies. As photographs are really necessary and better than all



descriptions for cortical localization, this chapter might be shortened considerably. The gyrus fornicatus is not described; the whole gyrus limbicus and the mesial margin of the cortex could hardly be understood by a novice from the description given on p. 19 and 27-29, nor would the relation of the N. amygdalæ become clear. These parts are not infrequently diseased, but clinically they are sufficiently unknown to excuse certain defects of this description (such as the statement that the granules of the fascia dentata are comparable with those of the cerebellum).

On p. 31, the fissura choroidea (a term used by v. Monakow for the choroid plexus connecting the fimbria with the thalamus) is said to form a very loose wall, forming a chief communication for the cerebro-spinal fluid between the lateral ventricles and the subarachnoid spaces. I have good evidence that such a communication is absent in a number of my cases (dilatation of lat. ventricles due to occlusion of the third ventricle, etc.); a positive demonstration of one is limited to small opening in the inferior horn (Key and Luschka). The study of the plexus is practically impossible with the simple embedding after v. Gudden; and in celloidin specimens I have never yet seen a communication.

With page 34, we enter upon the internal capsule and thalamus, subjects in which we owe so much to v. Monakow, and the whole anatomy of the midbrain and hindbrain follows. The description is in the main what can be seen with low powers in serial sections of normal brains, with comparison with the results of secondary degeneration. The general attitude is very conservative; the main lines are given from the results of the Gudden school, of which v. Monakow is undoubtedly the most active representative. To enter upon the differences between v. Monakow and Kölliker and others would lead too far.

On pages 90-99, v. Monakow sketches his histological views. He refuses Nissl's suggestion of a classification of nerve-cells according to the structure of the cell-body, adducing as an argument against it that the midbrain root of the fifth nerve was motor (with what proof he does not say), while Nissl is inclined to call it sensory merely from the structure of the cell. While Nissl's first classification can hardly be looked upon as more than an attempt in a worthy direction, if not carried out too dogmatically, v. Monakow's classification appears to be a step backwards. He follows Golgi with (1) neurones of the first category—cells with long neurites; (2) neurones of the second category—cells whose neurites lose their individuality after a short course

by dissolution; and he adds (3) neurones of a third category—Ramon y Cajal's cells of the cortex—with several short ascending neurites. He admits all the possible transitions between the first two categories. It would seem wiser to give up categories of this formal kind and to proceed to describe the known cell-types without an effort to force the unknown or incompletely known types into an *a priori* assumed number of categories. v. Monakow does not make a more than schematic use of his classification in the subsequent chapter on the general architecture of the nervous system. Chiefly from the point of view of experimental degenerations he gives us the types of gray matter, evidently without due references to more delicate stains than carmine. Apart from this defect, the method deserves great praise and might well be widely adopted in principle at least. So much attention has been paid exclusively to the 'neurone' that the study of the tissue as tissue is almost an unknown quantity to the modern generation—to its great disadvantage. Just in this direction, v. Monakow's work has a merit which greatly outdoes the few small defects mentioned above. It is his effort to bring before us true tissues such as he has learned to know them in his untiring experimental and pathological work. For the first time we find some of the most vital points in the understanding of nervous pathology made accessible in a hand-book. The importance of this step of v. Monakow is so great that we enumerate here his types of gray matter:

1. The type of the motor nuclei so-called, including the real motor nuclei of the spinal cord and brain-axis and also nuclei the motor character of which is not established: nucleus ruber tegmenti, Deiters' nucleus lateralis, v. Gudden's nucleus, the lateral nucleus of Burdach's columns etc.—(With the use of the Nissl method, this first type must necessarily be split into several types.) Section of the nerve-fibers coming from these cells causes the cells to atrophy (or at least to react in a characteristic manner).

2. The type of the gray of the sensory terminal nuclei. Degeneration of the afferent fibers causes the intermediate or ground-substance to atrophy and the cells of the nucleus to become more crowded. v. Monakow seems to put rather too exclusive weight on the presence and importance of the cells of Golgi's second category, especially in the paragraph speaking of

3. The type of the head and spinal ganglia, including the sympathetic.

4. The gray of the nuclei of the optic thalami and the parts dependent on the fore-brain—substantia nigra, certain elements of the

ant. corpus quadrigeminum and pons, the mesial part of Burdach's nucleus; Goll's nucleus, and the corpus Luyssii (the latter dependent on the corpus striatum). The ganglion habenulæ is an exception among the thalamic ganglia, as it does not depend on the existence of the forebrain. All these ganglia send the fibers in fascicles to the forebrain. After removal of the cerebrum the cells of these nuclei degenerate.

5. The gray of the cerebral cortex—for the first time presented in a text-book with illustrations of the results of the degeneration-method.

6. The gray of the forebrain-ganglia.

7. The gray of the substantia reticularis, characterized by meshes of medullated fibers. (Here v. Monakow classifies a second time the lateral nucleus, lateral part of Burdach's nucleus, nucleus of Bechterew; see my remark to 1.)

8. The central gray.

9. The gray of the cerebellar cortex.

10. The gray of the olive and the dentate nucleus.

11. The gray of the solitary cells (of the substantia reticularis).

12. Unclassified gray.

This classification gives many sound suggestions. Just as we became familiar with the fiber-tracts through their differences of growth and degeneration, so the law governing growth and degeneration of the types of gray matter throws the sparks of life into this step-child of neurology, the gray matter. The silver-method and the cell-stains will greatly help these methods, and they themselves depend ultimately on the degeneration-method more than Kölliker and others will admit, much to the disadvantage of their work. Another view of v. Monakow's deserves the heartiest commendation, viz., his emphatic statement, that the bundles of fibers composing the white substance are by no means compact strands of one type of fibers, but *always* mixtures, and objects of greater depth of study than is usually given them. The schematic plan of the architecture on p. 130 deserves special praise because it limits itself to the data which are experimentally established and leaves out even the best supported conjectures because they are mere conjectures and mentioned as such in the text only.

The second division of v. Monakow's introduction is devoted to a historical review of the physiology of the cortex, uniting the numerous conflicting data under the point of view of phylogenetic development. It is a splendid exposé of the laws of migration of function towards the cortex on an anatomical basis, and the completest

attempt to demonstrate physiologically *and* anatomically the cortical areas and sensori-motor mechanisms. On the whole, v. Monakow corroborates Tamburini in this and he adduces facts in favor of the general principle that motor (efferent) elements are grouped in smaller areas within the broader areas which receive afferent elements. The problem of restitution of cortical functions is ascribed to a more perfect utilization of the remaining nerve-elements both of the lower centers and the remaining cortex (perhaps with further growth of collaterals?). Vitzou's claim of extensive regeneration of cortex is discredited. Flechsig's association-centers are taken with much reserve, especially the posterior and middle ones; concerning the frontal lobes v. Monakow is inclined to see in them with Hitzig, etc., an organ of importance for psychic processes.

The third division of the introductory part deals with the general pathology of the central nervous system (p. 220-267). The short sketch of the pathological changes in the nerve-cells is hardly up to date (nor is the one of the neuroglia quite satisfactory) both in description and through the absence of a clear statement concerning the process of various *primary* lesions with their local reactions. The voice of v. Monakow becomes however clearly heard in the description of the secondary degenerations to which he devotes p. 237-267. This is a chapter which must be studied by everyone and contains a vast amount of essential data hardly known outside the Gudden school.

In the description of the secondary degeneration of central *nerve-fibers*, v. Monakow speaks of a transformation of the axis cylinders into naked neurites and later into sclerotic fibrils (p. 239). The degeneration of the *cells* is more likely to occur in the young and probably where there are not many collaterals which might have escaped the fate of the fiber (an argument used by Mahaim for the explanation of conflicting findings in the red nucleus). We cannot agree with v. Monakow concerning the statement that the same phases of secondary metamorphoses of the cells are found in the secondary degenerations as in the primary toxic or anaemic degeneration (p. 242). The difference is one of the best established data of neurocytology. The whole chapter is written from the experience furnished by the carmine method rather than the most recent stains of Nissl, Weigert, etc. It however compensates for its one-sidedness by the details of observation with this one method. The short résumé of secondary changes after destruction of a cerebral hemisphere, of partial lesions of a hemisphere, of the cerebellum, of the thalamus and subthalamic region,



pons, and medulla, will be recognized as a classical part of the work notwithstanding its relative shortness.

The fourth and last division of the introduction, the clinical symptomatology of organic brain-disease (p. 268-375) is remarkably good. It would lead outside of the domain of this journal to enter upon an account of detail. It is a classical presentation with only few omissions, well digested, not a mere encyclopædia of details.

Localization in the brain is the subject of p. 376-666, the second part of the work. It is an up-to-date review of the clinical and experimental material similar to Nothnagel's, and to Luciani and Sepelli's. The topics are: the forebrain (motor region, parietal lobe, visual sphere, frontal convolutions, localization and discussion of aphasia, foci of the internal capsule and corpus striatum), thalamus, peduncle, subthalamic region, tegmentum, midbrain, pons, cerebellum, and the forms of ophthalmoplegia.

The chapters on cerebral hemorrhage, encephalomalacia and sinus thrombosis (p. 667-884) are excellently presented.

By far the greatest number of illustrations are original, many of them of remarkable execution and beauty.

We turn next to the recent work of Prof. Mills of Philadelphia.<sup>1</sup>

"The great work of Gowers is the only extensive treatise on nervous diseases in the English language, although excellent manuals of moderate size have been written; and the author has hence been led to believe that a large text-book, including a comparatively full presentation of the many recent additions to the anatomy and histology of the nervous system, would be in accord with the needs of the profession."

The plan of the present volume (which will be followed by another should circumstances permit, including the remaining diseases of the nervous system, insanity, and the medical jurisprudence of both nervous and mental diseases) is as follows: (1) Sketch of the nervous system, its tissues, development, anatomy, physiology, nomenclature, and chemistry—p. 1-124. (2) General pathology and etiology, symptomatology and methods of investigation, electricity, and general therapeutics—p. 125-258. (3) Diseases of the membranes, sinuses and veins of the brain, and encephalic malformations and aberrations—p. 259-320. (4) Encephalic histology and physiology in their

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<sup>1</sup> C. K. Mills. *The Nervous System and its Diseases*. Diseases of the brain and cranial nerves, with a general introduction on the study and treatment of nervous diseases. With 459 illustrations. J. B. Lippincott Company, 1898.

relations to focal diseases of the brain—p. 321-415. (5) Diseases of the encephalic vessels, and the vascular disturbances of the brain—p. 416-555. (6) Residual encephalic lesions, degenerations, and diseases. (7) Affections of the special senses due to lesions and disturbances of the nerves of special sense and their correlated central structures—p. 667-794. (8) Disturbances of ocular movements due to lesions of the nerves, nuclei, and central apparatus of the ocular muscles—p. 795-851. (9) Diseases of the trigeminal and facial nerves and small cross-lesions of the pons and the pre-oblongata—p. 852-934. (10) Diseases of the postoblongata and its nerves—p. 935-1012.

This outline shows a somewhat unusual grouping of the topics, more like a series of independent essays than a text-book. It is indeed quite impossible to compare the book with Gowers or any other standard work. At first sight we see the familiar illustrations from other works and a fair number of original ones, largely diagrams, photographs of pathological specimens and cases, instruments, etc., on the whole in good execution. But in the text the writer follows an independent course.

The first chapter seems to address itself to a public which makes no claims to any elementary knowledge of any anatomy or histology. The chapter on the latter, for instance, opens with a description of the ovum of a cat. Whether a beginner would carry away as much safe and well arranged information as from Dana or Gowers must however be doubted. Mills adopts the nomenclature of Wilder. Besides giving a number of tabulated synonyms, he is obliged to give many explanations of terms in the text and, in many parts, the explanation of terms is more prominent than the description of the things which they designate. The reviewer admits his dislike for hybrids such as encephalo-spinal, where we have the correcter word cerebro-spinal, and terms like mediotemporal, medifrontal, where  $T_2$ ,  $t_2$ , and  $F_2$  and  $f_2$  have such a widely sanctioned use for second temporal and second frontal; or Wilder's subfrontal for  $F_3$  or 'preoblongata' for tegmentum, which term is alone used on p. 86. Mills 'aims to adopt improved names when this could be done without causing uncertainty or making too much explanation necessary, remembering that the book is for students and general practitioners rather than for anatomists and neurologists.' While fully recognizing the desirability of a simple and intelligible nomenclature, and certain merits and the perseverance of Wilder and his pupils, we should wish for the benefit of students or practitioners that a greater union of terminology might be reached, if possible, with less sacrifice of linguistic habit and taste. A true estimate

of the merit of the improved nomenclature of Mills could, of course, only be obtained through an acquaintance with the *didactic* results of this first part of his book.

A detailed criticism such as applied to v. Monakow's work, would lead us too far. On page 1 we read: "Scattered along some of these (peripheral) nerves are small gray masses of nervous matter called ganglia, some at least of which are also centers of energy; so that the central nervous system, while largely within the cranial and spinal cavities, is not strictly confined to them, but exists wherever nervous centres are found, etc." What follows on the first half dozen pages is hardly more than an enumeration of names of parts seen or not seen in the few surface drawings; with many inconsistencies of nomenclature. 'The chief subdivisions of the fully developed brain (page 2) are the cerebrum or great brain, the cerebellum or little brain, the pons, and the oblongata as shown in fig. 2. . . In fig. 3 it will be observed that the oblongata is divided into 2 portions, the postoblongata and the preoblongata (Wilder), the latter situated mainly between the pons and cavity of the brain known as the fourth ventricle. . . Both portions of the oblongata are composed largely of gray deposits or cell nests, while the pons is mainly constituted of nerve fibres or tracts, facts important to remember in connection with many points to be hereafter considered.' Then on page 4, under the heading 'Pons and Oblongata' we find about all the names of the things seen from the thalamus and chiasma backward—tuber cinereum, the 'postgeniculum' (the 'pregeniculum' being omitted) etc.

In the description of histology, obscure passages are rather frequent. 'It has usually been taught that nerve cells and nerve fibers are different structurally. Strictly speaking this is not true; they are parts of the same histological unit, as has been especially shown by recent investigation; but it is necessary for practical purposes to consider separately many of the facts relating to them.' Does 'different structurally' carry the meaning of 'not continuous'? The contact theory is expressed as follows: 'The cell and its processes are undoubtedly conductors of impulses; but the connection of nerve-cells with each other is physiological and not anatomical; it is by means of processes with processes or of processes with cells.' (p. 14). What follows is fully in keeping with the latter part of the sentence quoted.

Page 20 contains a discussion of which nerve cells are motor and which sensory. The latter are those 'in which the process has a shorter course and passes into a network or complex ramification of processes out of which the nerve fiber seems to arise.' On page 21

the sensory nerve-cells of the earth-worm have neuraxons and *dendrons*. The paragraph on neuroblasts and spongioblasts creates a sad confusion. The germ cells become neuroblasts and these become spongioblasts. Another picture of the situation is the following sentence (p. 27): 'The size of the posterior spinal ganglia is in the main proportionate to that of the nerves upon which they are formed.' The fact is true; but one might infer that the nerves are there before the ganglia are formed on them. The lateral nerve-roots of Gaskell (p. 28) arise from two columns of nerve cells, viz. the columns of Clarke and a column of the lateral horn. What idea is the student to form of the following sentences (p. 28): 'Every fiber of the gangliated system before it reaches its final destination fuses more or less with other fibers from the neuraxis. The Gasserian ganglion and other intracranial ganglia, as well as the posterior spinal ganglia have developed as offshoots of the encephalospinal nerves or nerve-roots close to their central terminations.' Then the development of the cerebral vesicles (p. 29): There are 3 primary vesicles. 'Soon the anterior and posterior vesicles each subdivide into two, one at each side(!) the middle remains single. These five vesicles give rise to the five rudimentary divisions of the brain—the forebrain, hindbrain, midbrain, interbrain and afterbrain'. And the flexures on p. 30!

As a motto for this entire anatomical introduction we might suggest the sentence on p. 70; 'In studying the cerebellum confusion may be caused through consulting different books, not only because of terminology, but also because of the different planes in which the views are presented.' And we should modestly suggest that after the use of one book we may create much confusion by confronting the student with an actual brain after he has been trained on figures and names only. The whole of pp. 1-94 is about the most confused conglomeration of terms and data imaginable. To pick out one instance: One might expect a student to know something concerning the *fillet* after reading this anatomy. The information is scattered over p. 5, 58, 62, 72, 82, 84, 85, 87, and amounts to this: on p. 5, where the lateral fillet is shown in the drawing of a brain-stem, it is called 'a white band constituting one of the important tracts between the spinal cord and the brain.' On p. 58, 'according to some authorities, the postcommissure is not a true commissure, but in part at least a decussation of the fibers of the fillet.' On p. 62, a small tract from Meynert's basal optic ganglion is 'supposed by some eventually to join the upper fillet, while in front it may be connected with the lenticular'. On p. 72, 'the dorsal longitudinal bundle and the fillet receive fibers from the



cerebellum, chiefly in the vermis, and connect the nuclei of the cranial nerves with the cerebellum. The fillet connects the cerebellum with the pons, the quadrigeminum and perhaps the striatum. The dorsal longitudinal bundle joins the fillet about the level of the olive, and both go into the antero-lateral tracts, and probably are thus connected directly with the ventral horn and indirectly with the ventral roots.' On p. 82, a drawing of the pons, 'modified from Kölliker,' shows a fillet extending from the raphe to the 'medipeduncle,' separating widely the trapezium and the superior olive. On p. 84, the lateral medullary tract (containing Gower's tract) is said to enter partly the lateral fillet. On p. 85, we find under the heading 'arcuate or arciform tracts': 'internal arcuate fibers constitute the discussion of the fillet; others from the clavate and cuneate nuclei pass through the dorsal longitudinal bundle and inferior olive to the fillet and restiform body of the opposite side.' On p. 87, the paragraph 'The lemniscus or fillet' contains only these data: 'It is divided into 3 parts, a division which probably goes to the parietal and lumbic cortex and hence has been called the *cortex lemniscus tract*; another subdivision which goes to the pregeminum and to the thalamus; and a lower *lateral division* which passes to the post geminum. It is a part of the great sensory tract, which is in the most ventral portion of the tegmentum. On its way brainward it gathers in the fibers which come from or go to the cell-nests of those cranial nerves which have sensory function.' This is all the student can hunt up on this important system.

So far the anatomical part. The part on architecture and general physiology, largely illustrated from van Gehuchten's work, might be more happily sketched.

The second chapter, on general pathology and etiology etc., is very brief in its neurological part; but gives long descriptions of all the possible instruments and, at the end of a rather full *materia medica*, 87 formulas with the customary and the metric weights. The part on pathology does not fulfill the expectations aroused by the first sentence of the preface. About all the work of the last 5 years seems to have been done in vain. The primary lesion in locomotor ataxia is attributed to the spinal ganglia. All the possible attributes of inflammation, degeneration etc., are enumerated, but what they are seems to be unimportant. I refer for instance to p. 127, where the various kinds of degeneration are 'explained.' The paragraph on phagocytosis is illustrated by a drawing from Obersteiner, in which pericellular spaces contain 'leucocytes.' The last few years have furnished fair

evidence for the neuroglia nature of these cells. The therapeutic part of this chapter contains so many valuable practical hints though that it will form one of the most attractive parts of the book for the practitioner; it is indeed so full that it might make many believe that the various measures could be learned from the book, if experience did not show that only practical training will make a masseur or an electrotherapist.

In a measure as we approach the clinical sides of the subject we feel that a practitioner of experience is the author of the work. The subjects of clinical teaching show the matured judgment, although even there an effort to bring in all the possible opinions of the various 'authorities' must prove confusing to most students, since, as a rule, obsolete views are put forth beside accepted ones without sufficient adverse criticism.

In connection with the various topics enumerated above, we find a number of special histological and physiological excursions which are on the whole far more satisfactory than the general sketch of anatomy. The paragraphs on the cerebral cortex give a résumé largely of a publication of Andriezen, a mass of details, unfortunately omitting practically everything that is essential just for those who do work on pathological changes of the cortex. A careful reader of the paragraph on the geniculate bodies (p. 358), if he is acquainted with the exact literature on these parts, will notice on what insufficient grounds Mills favors the refuted views of Darkschewitsch; and how much more concisely and accurately the matter could be stated. On p. 365, the unique view of Hamilton on the corpus callosum, never corroborated, is conscientiously reported with just as much emphasis as any other; it is even specially favored on p. 366, in a paragraph which is decidedly too 'suggestive.'

Chapter VI is of some interest to the anatomist. It begins: 'Acute focal diseases of the brain, such as hemorrhage, softening, tumor, and abscess, when they do not result fatally, leave cystic, necrosed, or sclerosed areas, and these [?] lead to progressive degenerations of the central and peripheral nervous system.'—'Secondary degeneration is set up and progresses chiefly in the conducting tracts along the lines in which they transmit motor, sensory, or other impulses. In the sensory systems it is ascending or centripetal—from the peripheral sense organs to the dorsal ganglia or cord [!] and from the cord to the brain' etc. Mills distinguishes secondary degeneration and involution (a retrogression which certain structures undergo as the result of disuse). The relatively simple 'laws' are not outlined. The reader learns that the fillet

can degenerate downward, but what this means is not explained. A few scattered cases from the literature are quoted but mostly not digested. The clinical part, hemiplegia, aphasia, etc., is given a rather full treatment.

Chapter VII begins with an enumeration of the cranial nerves. From here on the book contains short monographic articles of these nerves and their diseases, a counterpart to what was undertaken so splendidly by v. Frankl-Hochwart and others in Nothnagel's Handbook. We can only enter here on the anatomical and physiological introductions.

The olfactory. 'The short or reflex central path of the nerve, if such exists as a distinct path, is probably by way of the albicans and anterior portion of thalamus, while the cortical areas are the precallosal part of the gyrus fornicatus, the septum lucidum, and the inferior extremity of the hippocampal gyre and the uncinate gyre, and probably also the amygdala, the dentate fascia, and the stria of Lancisii.' This is a statement open to many criticisms; it is evidently made for the sake of having a long and a short path for each sense. On p. 668, much space is taken for the assertion that the olfactory nerve like the optic nerve is really part of the brain. This seems to come from a confusion of olfactory bulb and nerve. The olfactory nerve is built on the phylogenetically oldest plan of a sensory nerve, and does not even reach medullation. Burckhardt and many others have shown that it *comes* from the cells in the mucous membrane. Indeed Mills gives some of these data in the next paragraph and adds: 'The olfactory epithelium represents far more the origin of the olfactory fibers than it does their termination.' The data collected on the following five or six pages are furnished more directly from the sources, and on p. 670 the misstatements alluded to are given correctly with repetitions, followed by an 'abstract' from Kölliker on the central portion. Any unsophisticated student or practitioner will find himself overawed by the latter. The statement concerning the connection of the optic tract and the ganglion habenulae as described by Mendel is revived. Further we get continual references to the 'horn of Ammon' [sic]; if the student would try to get the synonym according to the 'improved nomenclature,' he could not do so in the rest of the work; it would remain a foreign body since everywhere else it is called hippocampus and he cannot be expected to understand fig. 341 on the ground of the general anatomy given by Mills.

P. 683-698 deal with the anatomy and physiology of the organs of taste. This summary is the clearest and best of the book, if we dis-

regard occasional accidents such as: 'cases have been recorded in which, *after* such lesion (division of the chorda tympani), the application of stimuli to the *distal* portion of the chorda tympani has caused sensations of taste in the region in which it was lost or impaired.'—Mills seems too ready to follow anatomical evidence in disputing the correctness of observations speaking for a participation of the fifth nerve in the taste perception; he does not even mention it among the 'accessory nerves.' In order to get rid of the cases of abolition of taste after lesions of the fifth, he suggests the possibility of simultaneous involvement of the central 'gustatory tracts passing in the pons from the oblongata to the cortex or in some cases even of the glossopharyngeal or pars intermedia of Wrisberg at or near the stem'. And 'in Horsley's operation by raising the temporal lobe it is possible to injure the cortical tract and centers for taste.' These 'possibilities' are practically impossibilities. The circumscribed defects of sensibility of taste on the tongue cannot reasonably be attributed to 'central' lesions; the motor apparatus suffers first and hemiparesis and hemianaesthesia would most likely occur in such a lesion of the pons before a limited hemiageusia; and a search in real specimens for the nervus Wrisbergii would have dispelled the idea that its fibers would very probably be injured without involvement of the seventh and eighth. Finally Horsley's operation would not under the worst conditions lead even to a complete 'central' deafness of the opposite ear and certainly not to limited hemiageusia, not even to a perfect hemiageusia, for which a complete decussation of the unknown tract and clinical evidence would be a condition.

The anatomy of the 8th nerve is very clearly described on ground of the data of Ramón y Cajal, Held and also Kölliker. A good original diagram gives an idea of the constitution of the eighth nerve (leaving undecided to which portion the neurones supplying the saccule go). By speaking of the "accessory nerves of hearing," Mills offers the physician material for a very fruitful conception of the auditory mechanisms as a sensory-motor apparatus of great complication. There are many reasons why the anatomist might consider Rauber's diagrams overdrawn and partly decidedly inaccurate. Fig. 350 contains fibers from the spiral ganglion reaching the posterior and the anterior opposite quadrigeminum. Fig. 351 'gives us a root fiber reaching the cortex, the only other constituent of the cortical tract coming from the 'nucleus of the lateral lemniscus,' while the best ascertained source, the internal geniculate body is omitted. In this instance the text is correcter than the diagrams borrowed. The portion on the vestibular



nerve is less exclusively anatomical and gives in part at least more clinical evidence.

The description of the optic apparatus begins with a comparison of the optic nerve with the posterior columns. The physiological and pathological similarities are evident; but it is incorrect to claim them also for the anatomical arrangements. In order to do this the common afferent neurone is described with van Gehuchten as follows: The posterior column process of the cell corresponds to the axis-cylinder, and the peripheral process to the dendritic process. Experimental tests, more important than speculative ones, would favor just the reverse conclusion (Lugaro, etc.) The retina is very well sketched. P. 750-753 are not distinguished by the same simplicity and clearness, since highly improbable and unessential connections of the optic nerves are mixed in promiscuously among the established facts. The support of the partial decussation rests much less on the clinical facts, than on this, that the experimental and pathological reaction of degeneration cannot be explained in any other way without throwing overboard the neurone-concept. As to the central localization of vision, Mills, unlike most of his countrymen, sides with Ferrier and Gowers without adducing adequate proof. Considering the amount of anatomical data available on the visual apparatus, Mills gives this part little attention.

Chapter VIII deals with the ocular movements. The introduction (anatomy, etc.) covers p. 795-809. The general review of the cranial nerves in this essay is largely based on Hill's plan. This is followed by an enumeration of the ocular muscles and the nerves supplying them, and by a description of the nerves and their supposed nuclei. It is of interest to compare this chapter with the corresponding one of v. Monakow, in its whole plan and spirit.

The remaining anatomical parts (trigeminal, facial, glossopharyngeal, pneumogastric, hypoglossal, pons and preoblongata, etc.) are largely based on Cajal and can hardly be said to facilitate the task of the student as much as ought to be the case with a better arrangement and digestion of the data of other writers as well.

A comparison between v. Monakow's work and the one of Mills is quite instructive. In Monakow we see one of the most experienced investigators of neural anatomy give a relatively very short account of the anatomy, physiology, and general pathology, and the great share to clinical data. Mills gives an apparently encyclopædic account of anatomical data from literature and allows anatomical concepts to govern the clinical part to a great extent, and instead of starting from clinical pictures, gives whole paragraphs on what might be observed on lesions of parts mentioned anatomically, but for which no clinical data are yet available. Either way has its special merits. In view of the controversies in anatomy and the great inclination towards tendential fabrications, the truly clinical method, with anatomy as a check, help and safe-guard, might form the safest guide for the practitioner. The presentation too becomes more logical. Not infrequently anatomophysiological claims have their best and only safe basis in clinical observations; and it seems odd to see on the contrary the clinical fact derived from the anatomical.

ADOLF MEYER.

## LITERARY NOTICES.

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### PHYSIOLOGY.

#### **Functional Changes in Nerve Cells.<sup>1</sup>**

The current fascicle of *La Cellule* contains two contributions to a subject of increasing interest, the physiology and pathology of the pyramid cells, with reference, in particular, to the retractility of their dendrites. The fact that these researches emanate from the laboratory of van Gehuchten at Louvain lends them additional significance, for upon this point van Gehuchten, of the few men entitled to speak with authority upon the Golgi method, has expressly reserved judgment. Cajal and v. Kölliker, on the other hand, have rejected the evidence in favor of retraction, on the ground that the so-called abnormalities are artifacts, due either to the imperfections of the method itself (Kölliker), or to faulty manipulation (Cajal and Lugaro). The recent literature upon this subject has, notwithstanding, become significantly voluminous and is constantly upon the increase. In the early stages of the development of this hypothesis, it was more or less contradictory and heterogeneous in character, since the specific function of retracility was associated by some with the axis-cylinders and their terminations, by others, with the dendrites and the gemmules. Demoor has the credit of having given to the theory the trend which it has since maintained, since he was the first to institute careful experiments upon animals, and to base his conclusions upon an observed increase in the number of varicosities of the dendritic processes, as compared with the normal animal. He maintained that these changes, physiological in character, as he believed, could be satisfactorily demonstrated by the Golgi method.

The first article of Soukhanoff is devoted to a reconsideration of the work of Demoor upon an experimental basis. Demoor had asserted

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<sup>1</sup> Dr. Serge Soukhanoff. 1. Contribution à l'étude des modifications que subissent les prolongements dendritiques des cellules nerveuses sous l'influence des narcotiques. 2. L'anatomie pathologique de la cellule nerveuse en rapport avec l'atrophie variqueuse des dendrites de l'écorce cérébrale. *La Cellule*. Tome XIV, 2 fascicule.

that the cerebra of dogs poisoned by morphine, choral, or chloroform, exhibited an extremely varicose condition of the dendrites. Lugaro and Azoulay had already questioned these conclusions, but Soukhanoff under the direction of v. Gehuchten has again put them to the test. From a series of eight experiments upon the effect of acute poisoning by ether, chloroform, and alcohol, upon three species of animals, the author concludes that the varicosity of the dendrites is not at all abnormal in amount. This renunciation of the territory won by Demoor is interesting in connection with the fact that Demoor himself, at the recent meeting of the physiologists in Cambridge, reiterated and emphasized his previous statements. Two other experiments, upon the action of trional on guinea-pigs, indicated a marked increase in the number of varicosities. In addition, Soukhanoff verifies the observation of Stefanowska, that invariably associated with the manifestation of retraction is the disappearance of the gemmulæ—"appendices piri-formes"—of the dendrites. The author interprets these changes as pathological in character, a specific atrophy, due to disturbances in nutrition.

The second article of Soukhanoff contains the result of experimentation upon the effects of acute and subacute poisoning by arsenic, of thyroidectomy, and of inoculation with hydrophobia, and tuberculin. A single control rabbit, supposed to be normal, was used for microscopic comparison. The effects of arsenic, as gathered from nine experiments, are, in general, the production of a condition of varicosity of the dendrite, with a corresponding disappearance of the gemmules. The amount of the change is very variable, and not at all proportional to the amount of poison injected, nor to the length of the period of poisoning. The lesion, as the author considers it, is diffuse, and not well localized either with reference to the layers or to the superficial areas of the cortex. The same, more or less indefinite, result, followed the inoculation of hydrophobia. The injection of tuberculin, and the experimental hydrophobia, produced the greatest alteration in the cortex; the number of cells affected, and the extent of the change in the dendrites, left no doubt as to the action of these agencies upon them.

These two articles represent perhaps the most satisfactory experimental evidence, save that of Lugaro (1897), for the theory of dendritic retraction. The constancy with which the changes succeed the action of any given agency, their significance from a physiological standpoint, and their diagnostic importance, are still, however, matters of great doubt.

R. WEIL.

## MORPHOLOGY.

The Organ of Jacobson in Mammals.<sup>1</sup>

This study was undertaken in part, apparently, for the purpose of clearing up the relations of the Hyrax to the Ungulates and Rodents, by an examination of the organ of Jacobson, which has marked differences in these two types. An examination of the characters which it presents in Hyrax, it was hoped, would clearly indicate the position of this obscure form. This expectation was fully justified by finding that both the grosser and finer structure of Jacobson's organ links this type rather with the Ungulates. The specimen used could not be exactly located as to species, but was a Namaqualand form closely allied to *Procavia capensis*. This is to be added to the already long list of rare types which Dr. Broom has studied with reference to the comparative anatomy of the organ of Jacobson. This study appears to be the first work done upon the organ in the hyracoidian Ungulates. In a previous paper the author has called attention to the two great types of the higher Mammalia in respect of the structure of Jacobson's organ. As his conclusions on this point are better stated there, though referred to in the present paper, we quote from it. "In the Prototheria we have an organ in a highly-developed condition, well supplied with glandular tissue, and having a large vascular plexus along its outer side. . . . The examination of the organ in the higher Eutheria also reveals some striking relationships. As a rule, the organ itself is more or less rudimentary, the plexus absent, and the glandular tissue much reduced. In the cartilages, however, it has been seen that there is almost invariably a peculiar and characteristic development by which any higher Eutherian in which the organ is developed, and in the majority of those even in which it is absent, can be at once distinguished from any of the lower mammals. In the complex development of the nasal floor cartilage we have, apparently, a thoroughly reliable character by which the higher Eutheria can be divided off from the lower into a distinct group by themselves. For this group I would propose the name *Cænorhinata*, while for those Eutheria which have the primitive arrangement of the cartilages of the nasal floor the distinguishing name *Archæorhinata* might be given. In the former group would be included the following orders: Primates, Carnivora, Insectivora, Chiroptera, and Ungulata; in the latter, the Edentata, and probably

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<sup>1</sup> On the Organ of Jacobson in the Hyrax, by R. Broom, M. D., B. Sc. One Plate. The Journal of Anatomy and Physiology, July, 1898, pp. 709-713.



the Rodentia."<sup>1</sup> The Hyrax according to this classification would belong to the group which he calls *Cænorhinata*.

H. HEATH BAWDEN.

### Ruge on the Facial Nerve.<sup>2</sup>

The motor portion of the seventh cranial nerve was studied in connection with the corresponding musculature in representatives of nearly all classes of craniote vertebrates in order to determine the homologies from the lowest Selachii to man. In view of the fact that in the lower vertebrates the seventh nerve is mainly sensory with a small motor component for the deep seated visceral muscles of the hyoid arch, while in the higher mammals it is almost wholly motor, and that too for the superficial muscles of expression of the face,—in view of this remarkable transformation, the task to which the author has addressed himself is one of extreme difficulty. The problem, however, is greatly simplified when we remember, on the one hand, that of the sensory facialis fibers of the fishes the greater part belong to the lateral line system and with the disappearance of this system all of these cutaneous fibers are in consequence totally wanting in higher vertebrates; and, on the other hand, that in the ontogeny of man the facial muscles of expression arise (as cited by Ruge from Rabl) in the neighborhood of the hyoid and hence are to be regarded as derivations of the hyoid musculature.

In the introductory general section the seventh nerve is shown to be in fishes a typical branchiomic nerve, like the ninth and tenth, supplying the spiracular cleft, and comprising a pharyngeal branch (r. palatinus), a pre-trematic branch (in some sharks) and a post-trematic branch (truncus hyo-mandibularis).

In the comparative anatomical section the selachians are treated with especial fulness and the attempt is made to derive all other forms from this. In the sharks we have (following Vetter) a system of superficial constrictor muscles in the region supplied by the facialis in which five members are designated; (1) a superficial dorsal maxillary portion; (2) a ventral mandibular portion; (3) a deeper dorsal hyoid portion; (4) a ventral hyoid portion; (5) a superficial dorso-ventral por-

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<sup>1</sup> A Contribution to the Comparative Anatomy of the Mammalian Organ of Jacobson. Trans. Roy. Soc. Ed., Vol. XXXIX, pt. i, 1897, p. 251-252 (a valuable bibliography is here appended).

<sup>2</sup> Ueber das peripherische Gebiet des Nervus facialis bei Wirbelthieren. By Dr. Georg Ruge. With 76 text-figures. Festschrift f. Gegenbaur, III, Leipzig, 1897, pp. 193-348.

tion running in front of the first gill pouch between (3) and (4). From these muscles the hyoid and facial muscles of higher forms are derived. Thus in man from (5) the following muscles are derived,—nasalis, caninus, bucco-labialis, triangularis oris, risorius Santorini. From (3) is derived the m. stapedius and from (4), with some question, the m. stylo-hyoideus. From (1) are derived the hinder belly of the digastric muscle and the platysma group, and from (2) the anterior belly of the digastric and the mylo-hyoideus.

The last two muscles are innervated from the mandibular ramus of the fifth nerve in mammals, reptiles, amphibians and bony fishes and the same is true for the muscles which probably correspond to these in *Ceratodus*. Now in order to bring these muscles into line as belonging to the facial segment, as distinguished from the trigeminal, Ruge has to assume that the trigeminal fibers innervating them are derived from the facial root—peripheral anastomosis in the case of the fishes and intra-cranial in the case of the higher forms, where peripheral anastomoses do not occur. The existence of such intra-cranial anastomoses is a pure assumption, and as for the bony fishes the reviewer can state from positive observation that the two muscles in question are supplied by fibers whose cells of origin are in the fifth nucleus and not in the seventh. Ruge's generalizations are therefore in this case too hasty and the morphology of these two muscles cannot be regarded as settled.

C. J. H.

#### Relation of the chorda tympani to the geniculate ganglion.<sup>1</sup>

The author undertook to determine experimentally the vexed question whether the gustatory fibers of the lingual nerve enter the chorda tympani, are connected with the cells of the geniculate ganglion and thus enter the brain through the portio intermedia of Wrisberg, or whether they enter by the fifth root or some other way, as many clinicians have maintained.

In adult dogs the chorda was pulled out after opening the middle ear and the animals killed after from 12 to 46 days. The normal and operated ganglia were hardened in sublimate after Heidenhein and stained in Delafield's hæmatoxylin. The ganglion cells of the operated side beginning with the 13th day showed the typical degeneration of Nissl. In cases, however, where a piece of the facial nerve one cm. long was cut out below the stylo-mastoid foramen the cells of the geniculate

<sup>1</sup> *Amabilino, Dr. Rosario*. Sui rapporti del ganglio genicolato con la corda del timpano e col facciale. Ricerche anatomiche sperimentali. *Il Pisani*, XIX, 1, 2, 1898.

must await embryological support. His views on some minor points, such as the morphology of the chorda tympani, also require revision. But this cannot be done within the limits of this review and these topics will be fully discussed in another place.

The paper is accompanied by a well chosen bibliography of 229 titles, and all vertebrate morphologists will be delighted to learn that this is but a fore-taste of a full bibliography of ichthyopsid neurology, containing titles of all of the extant literature, with abstracts, and indexes.

C. J. H.















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